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THE EXPANDING KNOWLEDGE OF MYCOLOGY
SINCE LINNAEUS.

IN preparing my last Presidential Address to you I had occasion to give some attention to most of Linnaeus's writings. The impression I gained from them was that, if certain philosophical considerations are disregarded, we are left with a surprisingly modern treatment of flowering plants, and, as I attempted to show, much of the theorizing is far less stultified than is generally supposed. When we turn to what he says about fungi, however, we find a different story—so different, in fact, that, so far as Linnaeus is concerned, we may consider that for all practical purposes mycology as a subject had not begun.

Fungi were mentioned by many of the classical writers—indeed, it would have been strange if such peculiar organisms had been entirely disregarded. In the days when most botanists were also classical scholars the numerous allusions to fungi in the classics were garnered, and it is rare now for any to be added to the store. As one would expect most of the interest in fungi was derived from their gastronomic effects, the surest way to empirical knowledge*.

Certain species gained a great reputation as delicacies†, and special rites attended their consumption in the period of decadent luxury at Rome‡; the passing of the sumptuary laws probably accounted for some of their popularity. Others

* Deaths due to eating fungi were not unknown. The earliest reference appears to be Eparchides (apud Athenaeus), who wrote an epigram relating how when Euripides was on a visit at Icarus, a woman, two grown-up sons, and a daughter were 'destroyed by pitiless fate in one day' through eating fungi.

Many rules were given for distinguishing edible from poisonous species; the belief in some of these, though they are utterly worthless, continues in this and other countries.

Several authors refer to the death of the emperor Tiberius Claudius after partaking of a dish of boleti 'prepared' by his wife Agrippina: Claudius descended into heaven (in coelum descendit) and so made way for another poison (venenum alterum) her son Nero, who used to commend boleti as food of the gods (ἱερῶν θεῶν).

† Particularly boletus (*Amanita caesarea*), fungi suilli (*Boletus edulis*), and truffles. It was safer to send a messenger with gold and silver and dress than with boleti.

Argentum atque aurum facile est, laenamque togamque

Mittere; boletos mittere difficile est.—MARTIAL, *Ep.*, xiii, 48.

‡ Pliny (Nat. Hist. xxii, Cap. 23) says that fungi are the only food which dainty voluptuaries prepare with their own hands and thus as it were feed upon them by anticipation, using amber knives and silver service. (Quando ipsae suis manibus deliciae praeeparant hunc cibum solum et cogitatione ante pascuntur, sucincis novaculis aut argenteo apparatu comitante.)

were held in regard because of a belief in their medicinal value, but classical writers were also interested in the strange manner of growth of fungi, and several marvelled at these plants without roots. They were regarded as due to the fermentation of the earth or its superfluous moisture or that of trees, decaying wood or other rotting things; and truffles were generally thought to owe their formation to the action of lightning during thunderstorms.

The writers of Herbals in this as in other botanical matters stuck rather closely to classical authority. But before long such authority began to give way to observation, if indeed it can truly be said that it was ever blindly accepted except as an explanation. Caesalpinus in his *De Plantis*, 1583 (Lib. xvi, Cap. xiv, p. 28), writes: 'Some plants have no seed; these are the most imperfect, and spring from decaying substances; and they therefore have to feed themselves and grow, and are unable to produce their like; they are a sort of intermediate existences between plants and inanimate nature. In this respect Fungi resemble zoophytes which are intermediate between plants and animals, and of the same nature are the Lemnae, Lichens and many marine plants.' Here we have a fairly clear statement about the spontaneous generation of fungi and a suggestion that fungi are not plants—two ideas that later played a large part in botanical discussions.

Five years later, 1588, there is a statement by Porta which is worth noting. In his *Phytognomonica* (Lib. vi, p. 240) he has a chapter with the heading 'Contrary to the opinion of the Ancients all plants are provided with seed'. In it he writes, 'From fungi I have succeeded in collecting seed, very small and black, lying hidden in oblong chambers or furrows extending from the stalk to the circumference, and chiefly from those which grow on stones, where, when falling, the seed is sown and sprouts with perennial fertility. Falsely therefore has Porphyrius said that fungi, since they do not arise from seed, are the children of the gods. So also in Truffles, a black seed lies hidden. On this account, they come forth in woods where they have frequently been produced and have rotted away. And I have often seen them arising where the washings of tan or the tan itself is thrown away.' Doubtless Porta recognized the spores of some of the dark spored forms such as *Coprinus*. The truffle on tan was obviously the Mycetozoa *Fuligo septica*, the 'flowers of tan'; this produces clouds of spores, and apparently Porta recognized these as being the same structures as he had noticed on gills.

It is obvious that further progress waited upon the possibility of closer observation than could be accomplished by the aid of a simple lens. With the invention of the microscope it

was possible to make this closer observation, but progress was slow : there was much to observe and observers were few. Robert Hooke's *Micrographia or some Physiological Descriptions of Minnute Bodies made by Magnifying Glasses. With Observations and Enquiries thereupon* was published in 1665. Fungi were among the great variety of objects which he examined with his microscope ; two sections relate to them, one (Observ. 19) ; ' Of a Plant growing in the blighted or yellow specks of Damask-rose-leaves, Bramble-leaves, and some other kind of leaves ', the other (Observ. 20), ' Of blue Mould, and of the first Principles of Vegetation arising from Putrefaction '. The rose blight is the rust *Phragmidium*, and the description is accompanied by the first known illustration of a microscopic fungus [Pl. 5, b]. Hooke did not recognize the true significance of the teleutospores, but interpreted them ' like Seed-cods ', though he did not observe any seeds within them.

His views on plant disease were that ' Though the original cause, or seminal principle from which this minute Plant on Rose leaves did spring, were, before the corruption caus'd by the Mill-dew, a component part of the leaf on which it grew, and did serve as a *coagent* in the production and constitution of it, yet might it be so consummate, as to produce a seed which might have a power of propagating the same species. . . . So that the little cases which appear to grow on the top of the slender stalks, may, for ought I know, though I should suppose them to spring from the perverting of the usual course of the parent Vegetable, contain a seed, which, being scatter'd on other leaves of the same Plant, may produce a Plant of much the same kind '.

Several moulds are mentioned in the other section : ' The Blue and White and several kinds of hairy mouldy spots, which are observable upon divers kinds of *putrify'd* bodies, whether Animal substances, or Vegetable, such as the skin, raw or dress'd, flesh, blood, humours, milk, green Cheese, etc. or rotten sappy Wood, or Herbs, Leaves, Barks, Roots, etc. of Plants, are all of them nothing else but several kinds of small and variously figur'd Mushrooms, which, from convenient materials in those *putrifying* bodies, are, by the concurrent heat of the Air, excited to a certain kind of vegetation, which will not be unworthy our more serious speculation and examination '. He figures a small white speck of hairy mould which he found growing on the red sheepskin cover of a book [Pl. 5, a]. This was probably a *Mucor*, but here as elsewhere ' what these heads contain'd I could not perceive ; whether they were knobs and flowers, or seed cases, I am not able to say '. Hooke's views of fungi are thus expressed. ' First, that Mould and Mushrooms require no seminal property, but the former may be produc'd at any time from any kind of *putrifying*

Animal, or Vegetable Substance, as Flesh, etc. kept moist and warm . . . Next, that as Mushrooms may be generated without seed, so does it not appear that they have any such thing as seed in any part of them; for having considered several kinds of them, I could never find any thing in them that I could with any probability gness to be the seed of it, so that it does not as yet appear (that I know of) that Mushrooms may be generated from a seed, but they rather seem to depend merely upon a convenient constitution of the matter out of which they are made, and a concurrence of either natural or artificial heat'. We find similar ideas about the nature of fungi and fungal disease extending over the next century and a half, in spite of the gradual accumulation of knowledge.

We owe to Hooke our first knowledge of the internal structure of the larger fungi; this is hidden away in his section of sponges, Examining several kinds of mushrooms he found 'their texture to be somewhat of this kind, that is, to consist of an infinite company of small filaments, every way contex'd and woven together, so as to make a kind of cloth'; and 'Touchwood' or 'Spunk' 'a kind of Jews-ear' (presumably amadou—that we meet with to be sold in Shops, is brought from beyond Seas')—he found 'the texture of this Touchwood seems more like that of a Lock or a Fleece of Wool, for it consists of an infinite number of small filaments . . . The filaments I could plainly enough perceive to be even, round, cylindrical, transparent bodies, and to cross each other every way'*.

Micrographia was published by the Royal Society of which Hooke was secretary. It is interesting to note that the first of the famous letters written by A. van Leeuwenhoek to the Society (1673-1723) began with an observation on 'the Mould upon skin, flesh, or other things'†. There is nothing noteworthy

* Another reference to fungus structure occurs in the well-known Observ. XVIII. Of the *Schematisme* or *Texture* of *Cork*, and of the Cells and Pores of some other such frothy Bodies, where it is stated that 'Cork seems to be by the transverse constitution of the pores, a kind of *Fungus* or *Mushrome*'.

† The account in *Phil. Trans.* VI, 6037 (1673) reads, 'The Mould upon skin, flesh, or other things, hath been by some represented to be shott out in the form of the stalks of Vegetables, so as that some of those stalks appeared with round knobs at the end, some with blossom-like leaves. But I do observe such Mould to shoot up first with a straight transparent stalk, in which stalk is driven up a globous substance, which for the most part places it self at the top of the stalk, and is follow'd by another globul, driving out the first either side-ways, or at the top, and that is succeeded by a third and more such globuls; all which make up at last one great knob on the stalk, an hundred times thicker than the stalk it self. And this knob indeed consists of nothing else than of many small roundish knobs, which being multiplied, the big knob begins to burst asunder, and then represents a kind of Blossoms with Leaves.'

in the summarized account unless the 'globous substance' driven up the stalks is an observation and not a deduction, for if Leeuwenhoek saw a movement it must have been the streaming of the protoplasm. Leeuwenhoek not only discovered bacteria and protozoa but also yeasts. These he described in a letter in 1680* to Thomas Gale, Secretary of the Royal Society. In examining beer yeast he generally found that it consists of globules floating in a clear medium. Each globule of yeast looked as if it enclosed six distinct globules of the same size and shape as human blood corpuscles. Examining beer at the time it was poured from the cooling vessels into the fermenting tin he saw that it contained a great many small particles. 'Some of these seemed to be quite round, others were irregular, and some exceeded the others in size, and seemed to consist of two, three, or four of the aforesaid particles joined together. Others again consisted of six globules and these last formed a complete globule of yeast.' He failed in his endeavour to see how the globule combined. What he doubtless saw were aggregates of yeast-cells due to rapid budding.

A few years later the Royal Society published *Anatome Plantarum* by M. Malpighi. In the second part (1679, p. 62) is a section headed 'De plantis quae in aliis vegetant', which deals with Fungi, together with Mistletoe, Lichens, Mosses, etc. His descriptions are illustrated by a plate [Pl. 5, c] with twenty-four sketches of moulds, which he calls *Mucedo*, and three of an agaric, which he calls *Fungus*. The figures show that the moulds he found growing on second-rate cheese, on the putrescent pericarp of melons, on lemons and oranges, on wood, and on bread, include *Rhizopus stolonifer*, *Mucor*, *Penicillium* and *Botrytis*.

He describes the development of the sporangia of the first two and figures the spores in most of them. He also shows what appears to be a septate mycelium. He interprets the sporangiophore as an inflorescence and the spores as florets. He describes the development of a small agaric growing on wood, noting the network of hyphae from which the fruit-body arises by the uniting of the filaments to form a stalk. After remarking upon the fact that the plants he has treated in the section derive nutriment from the substratum, and that Mistletoe is propagated by seeds, he states that it is unknown how the others arise and multiply,

* Published in Dutch, 1684, and in Latin, 1695. In the Latin edition of Leeuwenhoek's works, 1722, the letter is headed 'De fermento cerevisiae. De bullulis aëreis ex eo propullulantibus. Ut & ex oculis cancerorum'. The relevant portion of the original letter is reproduced in a paper by A. Chaston Chapman in *Journ. Inst. Brewing*, xxxvii, pp. 433-6 (1931).

especially Fungi and Mucedo. He holds that 'either Fungi, Mucedo and Moss have their own seed, by which their species is propagated, or they sprout from the growth of fragments of themselves as happens in other plants', adding that the frustules may be distributed by the wind.

We may regard as the next step the clear recognition of the mycelium or spawn of mushrooms. The first account we have of mushroom growing* is by J. P. de Tournefort in 1707, the year of Linnaeus's birth. It is remarkable that, except for the inoculation of the beds, the process has altered little since then [Pl. 5, e]; during the last thirty years the so-called pure culture methods have been evolved to replace 'virgin spawn' previously used for this inoculation. We do not know when the system of raising mushrooms was begun in Paris, but it was probably before 1678, for in that year Marchant exhibited mouldy horse droppings and demonstrated how the white mycelial strands swelled at their ends to produce mushrooms †.

Tournefort held that the Parisian method of raising mushrooms favoured the idea of those who believed that they arise from seed the same as other plants. He describes the mycelium and how it gives rise to mushrooms. 'According to appearances these white threads are nothing other than developed seeds, or germs of mushrooms, and all these germs were enclosed in the horse droppings in so small a volume, that one can only perceive them whatever care one takes, after they have grown out into little hairs.' In the report to the French Academy on Tournefort's paper the anonymous writer says that 'without fear we can advance the view that all fungi have seeds', but four years later we find the younger Marchant describing *Xylaria polymorpha* as a terrestrial Lithophyte (*Lithophyton terrestre digitatum nigrum*) because of the perithecia containing 'seeds'.

* The common field mushroom (*Psalliota campestris*) is the only species cultivated on a commercial scale in Europe, although many unsuccessful attempts have been made to grow truffles and other edible species. In Japan the Shiitake (*Cortinellus Shiitake*) is cultivated commercially. *Volvaria volvacea* is grown in widely separated areas of the tropics, but the prepared vegetable refuse heaps are not artificially inoculated. There are many accounts of the ancient cultivation of *Pholiota aegerita*: Dioscorides says that if we 'bark the white or black poplar, cutting the bark into pieces, and covering it with horse-dung, an excellent kind of fungus will spring up, and continue to bear throughout the year'.

† According to Persoon, *Traité sur les Champignons*, p. 15 (1818), it was this demonstration that originated the method. 'L'origine de la culture de cette espèce est due à Marchand, le père, qui fit voir, en 1678, à l'Académie, la première formation de ce champignon dans les érotins moisies, comme des filets blancs, dont les extrémités se grossissent en champignons.'

In spite of Tournefort's clear description there was still far more speculation than certainty about the nature of fungal mycelium. One of the works which had great influence on contemporary thought was that of L. F. Marsigli (1714), who was a sufficiently keen mycologist to study fungi on the battlefield. He disbelieved that fungi were reproduced from seeds. He regarded the 'grana quaedam minima' as insect ova, and held that fungi originated in corruption—discussing at length the possibility of the peridiola of *Fungilli calcyformes seminiferi* [*Cyathus Olla*] being seeds decided they were frustules—... semen autem est foetus non pars, propria peculiaris pars*. Fungi occur where there is fatty substance, consisting of some sort of oiliness mixed with nitrous salt, which penetrates through the roots and between the fibres of the wood by means of a fermentation caused by mild warmth and dampness. The ligneous matter becomes transformed into a compact substance, which insinuates itself either between the wood and the bark, or through the pores of the bark, and engenders woody fungi [Pl. 5, d]. The same product of fermentation coagulates in the ground and becomes the *situs*, which swelling and emerging above the surface acquires the nature and form of toadstools †.

Marsigli dedicated his dissertation to J. M. Lancisi, who agreed with his interpretations in all essential points ‡.

Lancisi asserted that plants considered to be dead still retain their juices which can resume their activity in the construction of new forms. From these juices fungi originate; they cannot arise from purely inorganic substrata, but when they are formed on soil this actually contains a number of organic patches. He has no doubt that the subobscura corpora on the gills are part eggs and part faeces of particular insects §.

* Cf. Haller (1768), who regarded the peridioles as 'vivipara generatione ex planta matre productae'. Schrank (1789) remarked of the two species of *Cyathus* he described 'Sie sind, da ihre Linsen der Embryonen der Künftigen Generation sind, der *Volvox globator* des Pflanzenreichs'.

† Marsigli's 'Omnium epilogus' reads:—'Origo prima e ligno, & accedente succo madentis terrae (haec fimo jam putrefacto non deest) initioque spuma lentior (haec Situs corpuscula) deinde corpus membranæ simile (hoc Situs filamenta in crustam efformata) deinde partus (hic Fungi).'

‡ This *Responsio* was published in the same volume together with two other discourses by him.

§ *Cyathus* figured largely in the discussions about the seeds of fungi. J. Goedart (1662) was decided in his opinion. In his section on spiders he says: 'There is another kind of *Mushroom*, which rises from the Earth, which first of all appears shut, but in a days time is open, and then it represents the forme of a *Mushroom*, with a round dish, or little house, like the cup out of which the *Oake Acorns* are taken; in this Cup is found Five round grains of seed, of the size of Raddish-seed, but pellucid, as *Christall*; after these grains fall out of the cup on to the

Marsigli's illustrations show clearly that the mycelium was recognized, but it was entirely misinterpreted as an intermediate stage between corruption and the formation of the fungal fruit-body.

The peculiarities of the growth of fungi thus led to interpretations which in no way satisfied those who were convinced that fungi were constant in their structure. Thus Antoine de Jussieu (1728), in a paper entitled 'De la nécessité d'établir dans la méthode nouvelle des Plantes, une Classe particulière pour les Fungus, à laquelle doivent se rapporter, non seulement les Champignons, les Agarics, mais encore les Lichen . . .', stated that though fungi have not that general analogy with plants which permits of their being classed with them, there is less difference among them than amongst plants of different classes; their only resemblance is with lichens. Lignicolous and terrestrial species have the same essential structure, and, as species are the same no matter when or where collected, it is obvious that they must be reproduced by seeds. 'This supposition of seeds is not imaginary; they are felt by touch, like meal, in those fungi where the cap has leaves beneath; especially when they begin to decay; one sees them easily with the aid of a lens in those whose leaves are black at the margin; one finds them in the form of a powder in those that are called *Lycoperdon*, they appear in fairly large grains, on the Champignon de Malthe *, they are placed in chambers destined to contain them in Hypoxylon.'

The following year, 1729, marks an epoch in our knowledge of fungi, when P. A. Micheli published his *Nova Plantarum Genera*. The genera were arranged according to Tournefort's method, so reads the title—'with additional notes and observations on the planting, origin, and growth of fungi, mucors and allied plants'. Micheli was the first to pay

superficies, or into the chinks of the earth; they are cherished by the heat of the sun, till they begin to live, afterwards they get feet; and in three years time they attain to their full growth, all these things I tried twice Two years together'. (M. Lister's Translation (1682).)

Camerarius (1688) and others failed to obtain growth when they sowed the peridiola.

Ray, in his *Historia Plantarum*, III (1706), replying to criticisms of his negative characterization of fungi, says regarding *Cyathus* 'verum ut demus unam vel alteram Fungi speciem seminiferam esse (de quo tamen est cur quis dubitat) *Una Hirundo*, ut aiunt, *non facit Ver*.'

* This is the *Fungus Typhoides coccineus Melitensis* of Boccone (1674), the *Fungus Mauritanicus verrucosus, ruber* of Petiver (1702). Lancisi held that it was a fungiform plant rather than a fungus because it had seeds. Micheli showed that it was a flowering plant, and named it *Cynomorion* [*Cynomorium coccineum* Linn.: Balanophoraceae]. Its medicinal properties were described by Galen and Dioscorides and were the subject of one of the *Amoenitates Academicæ*—*Fungus Melitensis* (Resp. J. Pfeiffer), 1755.

special attention to the group as a whole, and his harvest was amazing*. Some of his new genera of fungi were *Polyporus*, *Aspergillus*, *Clathrus*, *Mucor* and *Geaster*; his *Puccinia* is the modern *Gymnosporangium*. His investigations dealt with flowering plants, liverworts, mosses and lichens in addition to fungi†, and his researches on the last were doubtless guided by a desire to discover flowers and seeds so that fungi might be brought into line with flowering plants. He found his 'seeds'‡ in all kinds of fungi—Polypores, Agarics, Gasteromycetes, Discomycetes, Truffles and Moulds. Further, he observed that the spores of some agarics are arranged in fours on the surface of the gill, though in others they appear to be scattered irregularly§. In spite of the fact that the quaternary arrangement of the spores was clearly seen no suggestion is made, however, that they are borne on basidia. There is no indication of the species in which the different arrangements are figured—plate 73 is the first of those devoted to agarics and illustrates the general description. As the arrangement in fours is easiest to see in dark-spored forms such as *Panaeolus* it is probable that one of these is figured, and that the irregular arrangement was seen in species of *Coprinus* where there is dimorphism or even trimorphism of basidia—the basidia being of different lengths. This is partly borne out by the fact that one of the other three drawings of gill-faces shows the irregular arrangement of *Coprinus narcoticus* (Pl. 79, fig. 4):

* The first monograph on fungi was *Fungorum in Pannoniis observationum brevis Historia* by Clusius (Charles de l'Escluse), one of the five complementary sections of his *Rariorum Plantarum Historia* (1601). Previously little or nothing had been added to the accounts given by classical authors. It comprises twenty-eight folio pages and thirty-two woodcuts, all except two (copied from l'Obel) original. ['In Pannoniis' refers to the Roman province of Pannonia, bounded on the north and east by the Danube, and comprising portions of Austria, Hungary and Yugoslavia.] The first volume entirely devoted to fungi—even to cryptogams—was F. van Storbееck's *Theatrum Fungorum* (1675). More than half of Storbееck's engravings are copied from the Code de l'Escluse, a collection of 221 coloured paintings of fungi, which Clusius had had prepared to aid him in his descriptions; the Code is preserved in the Library of Leiden University.

† Micheli's herbarium and drawings of the larger fungi, mostly coloured, with manuscript notes, are in the Botanical Institute, Florence.

‡ Referring to ancient writers Micheli remarks that the account by Petronius in his *Satiricon* of the extravagant tastes of the gourmand Trimalchis, who wrote to India for some seed of the boletus as 'quidam per jocum': he refers also to the statement by Theophrastus that some think that truffles are produced from seed, because those which grow on the shore of the Mityleneans appear only after floods which bring down the seed from Trarac where many truffles are found.

§ 'In aliquibus singillatim dispersa G (Tab. 76 c) in aliis quaterna sibi contigua H.' The plate number is wrong; it should be 73. This plate is dedicated to James Sherard, the brother of William Sherard who founded the Sherardian Professorship of Botany at Oxford [Pl. 5, f].

but that of *Volvaria gloiocephala* (Pl. 76, fig. 1), a pink-spored form and the other a dimidiate agaric, probably *Crepidotus* (Pl. 65, fig. 5), also both show the irregular arrangement.

In his search for flowers Micheli discovered the hairs on the edges of the gills of some species. These marginal hairs or cystidia he interpreted as apetalous flowers. At the margin of the laminae apetalous flowers arise, naked, consisting only of a cylindrical filament; in some species solitary or distinct from one another, in others, however, collected into a mass or tuft. He thus considered the flowers to be situated on the edge of the gill far from where the seeds are formed, a strange view nowadays, but not so at the beginning of the eighteenth century.

Another of Micheli's discoveries was that of cystidia on the gill surface of many species, particularly those growing on animal dung (species of *Coprinus*, e.g. *C. ephemerus*), and he correctly interpreted their prop-like function in keeping the gills apart. These conical or pyramidal transparent bodies 'are made by a wise device of nature so that one lamella does not touch another lest by chance the seeds produced between them shall be hindered in their development and they should not fall only where they ought to fall'.

In addition to noting the definite arrangement of spores in some agarics Micheli also observed asci for the first time. He figured these in one of the lichens he described, but says he could not find seeds. In truffles, however, he figured and described asci containing spores, noting the variations in number characteristic of these fungi*.

Micheli was not satisfied merely with the belief that seeds are present in fungi, but went further by carrying out a series of experiments which he called 'observations' to see whether the bodies he interpreted as seeds would give rise to the same species of fungus which bore them. For these experiments he used *Fungus* [*Agaricus*] and the three common moulds *Botrytis*, *Aspergillus* and *Mucor* [Pl. 6, a]. He planted the spores of the agaric on dead leaves and those of the moulds on freshly cut pieces of melon, quince, and pear [Pl. 6, b]. The experiments with moulds were immediately successful, and the spores were again sown and the same fungi again obtained; the experiments were repeated and varied with convincing results. The agaric needed a much longer time for any result; some months after sowing the spores a mycelium was seen on some of the leaves and later gave rise to the fruit-bodies of the fungus.

* 'Capsulis D vesicæ in morem mollibus, subrotundis, ac minutissimis ubique infecta, in quarum singulis continentur modo bina E, modo terna F, modo quaterna G, rotunda, vel subrotunda, & verrucosa semina H.' (Tab. 102) [Pl. 6, c].

It might have been expected that Micheli's work would have aroused a great deal of interest in fungi, for it showed beyond all doubt that they are entities and not degeneration products. Most botanists, however, were—and remained—of the opinion expressed by Sébastien Vaillant in 1718—the paper from which Linnaeus got his first ideas about the sexuality of plants. Vaillant gave them up as hopeless, and certainly did not favour the classical idea that they were the food of the gods, if not their children. 'Je sape entierement . . . ces captieuses Fleurs sans fleur, race maudite, qui semble n'avoir été créée ou inventée que pour en imposer aux plus habiles, & désoler absolument les jeunes Botanistes, lesquels en étant débarassez, se trouvent d'abord en état d'entrer tête levée dans le vaste empire de Flore'*. Can it be that these remarks affected Linnaeus? We know that the ideas contained in the paper had a considerable influence on his career and scientific development, and he was at the most impressionable age when he read it.

It is difficult to understand the attitude Linnaeus adopted towards fungi. Despite the opinion of many of his contemporaries he had a very receptive mind, and was ready to study any problems or to believe any statement not contrary to his knowledge.

To explain Linnaeus's influence on mycology it has been necessary to consider in some detail the gradual development of ideas about the nature of fungi. Linnaeus had an extensive knowledge of the work of his predecessors—if his writings did not show this we have the evidence of his library—but it must be admitted that he did not advance the study of mycology, and it might even be said that he definitely retarded it.

In *Systema Naturae* (1735), in 'Observationes in Regnum Vegetabile', nine genera are listed with their synonyms—*Agaricus* D, *Amanita* D; *Boletus* D; *Hydna*, *Erinaceus* D; *Merulius* B, *Morchella* D; *Elvela*, *Fungoides* D; *Peziza* D, *Cyathoides* M; *Coniplea*, *Lycoperdon* T, *Lycoperdastrum* M, *Geaster* M, *Carpobolus* M; *Byssus* Rj; *Nostoc* V†.

Strange to say Linnaeus's best work on the subject is contained in *Flora Lapponica*, which, published in 1737, gave an account of his journey five years previously. Here he gives short diagnoses of forty-seven species of *Agaricus*, apparently drawn up on the spot, and excuses himself for not giving synonyms because of the difficulty of preparing

* Vaillant later seems to have viewed these lawless, sexless creatures with less disdain, for in his *Botanicon Parisiense*, published posthumously in 1727, he gives a remarkably good presentation of cryptogams. Like his predecessor Tournefort he apparently was engaged on a special study of fungi at the time of his death.

† D = Dillenius, B = Boerhaave, M = Micheli, T = Tournefort, Rj = Ray, V = Vaillant.

herbarium specimens of these fleshy forms * and of scrambling over cliffs and rocks carrying the necessary books. It is obvious that on his journey he paid considerable attention to fungi, and he suggests that only a few were dealt with: he had the use of Kudbeck's coloured drawings of Lapland fungi. He divides his genus *Agaricus* into sixteen sections, but is unable to make generic distinctions in the innumerable species because of their variability †. The other fungi he describes are five species of *Boletus* ‡, two species of *Hydna*, two of *Lycoperdon*, seven of *Byssus* and one of *Mucor*. Here full references to other authors are given. There is a long account of fifteen flies which deposit their eggs in agarics §, which is a sufficient answer to Tiling's theory (1683) of the metamorphosis of these fungi into insects. Other notes describe special points about growth, habitat and uses. In the note on the species of *Mucor* he says that he had neither the eyes, the literature nor the opportunity to examine the other species of the genus.

Linnaeus made his Lapland tour when he was twenty-five years of age, and his account of Lapland fungi is such that it suggests that he had a real interest in the subject.

In *Genera Plantarum* (1737) he lists eleven genera—*Agaricus*, *Boletus*, *Hydna* (corrected to *Hydnum* in *Methodus sexualis* which is appended to the work), *Elvela*, *Clavaria*, *Clathrus*, *Byssus* and *Mucor*. Unlike his predecessors Linnaeus did not trouble about the proper application of classical names. Thus the boletus of the Romans he called *Agaricus*, whereas the agaricus of classical times was a fungus which grew on trees, probably *Daedalea quercina*. In *Hortus Cliffortianus*, also 1737, he gives six genera with eight species.

Linnaeus about this time was much influenced in his opinions about fungi by the famous Swiss scientist Albrecht von Haller, who wrote to him in December 1737 'I have, this autumn, met with many species of *Lichen-Agaricus* [*Sphaeria*], of various forms; but in every one there are globules full of pollen (rather seeds), ranged under some sort of bark . . . I have

* 'Tum quod post exsiccationem, quae hic difficillima erat, vix eundem liceat dignoscere fungum.'

† 'Attamen cum viderim unam eandemque speciem ligno insidentem evasisse Agaricum, alterum vero individuum ex eodem semine Amanitam, ex eadem specie diversa non constitui genera.'

‡ That Linnaeus had a sense of humour is seen from many of the descriptions in *Systema Naturae*. A note on *Boletus acaulis, superne laevis, salici insidens* [*Trametes suaveolens*] is probably not so well known: 'Adolescentes hunc inventum sollicitè servant in marsupio ante pubem pendulo, ut gratiorem odorem spirantes nymphis suis placeant. O ridicula Venus, tibi, quae in exteris regionibus uteris caffee & cocholata, conditis & saccharatis, Vinis & bellariis, gemmis & margaritis, auro & argento, serico & cosmetico, saltationibus & conventiculis, musica & comoediis, tibi sufficit hic solus exsuccus fungus.'

§ Cf. *Pandora insectorum*, 1758 (Resp. E. O. Rydbeck).

caused several *Fungi*, near 150, to be delineated in their proper colours, and I shall go on with this undertaking. I have noticed, in many of them, the seminal pollen, of a black, blue, or other colour; but never any vestiges of the flowers as described by Micheli. Whenever I have time, I will examine these plants microscopically'. The following month he writes 'As I intend to give an entire history of the *Fungi*, it cannot go to press before November': in November he says 'The *Fungi* prove excessively troublesome'. In January 1739—Targioni continues to threaten us with the publication of Micheli's second volume*, for which purpose he certainly has money enough. No doubt Micheli has great merit, but his work contains many trifling things, and too many varieties, especially among the *Fungi*'. Announcing the sending to press of his *Synopsis* †, August 1740, he calls fungi 'a mutable and treacherous tribe'. In September 1740 he writes, 'I have detected a very curious elastic motion in the common sessile *Peziza* ‡, of a dirty white hue. The whole plant contracts spontaneously, and discharges a powder upwards, with a sort of hissing noise. This doubtless is the seed. The *Clathroides* § are also elastic, and their dust is expelled spontaneously, though more slowly. I have discovered no flowers of *Fungi*'. Linnaeus was enthusiastic about Haller's account of fungi, and wrote in July 1743: 'You have found out a new world among the *Fungi*. You have shown the way through the wilderness, where no one before could find any certain paths. Dillenius || and Micheli are nothing in *Fungi*. We owe everything to Haller, who has accomplished a work of immense labour'.

Haller's account of fungi is important from a taxonomic standpoint, but it is not my purpose to deal in detail with the development of this aspect of the subject.

Linnaeus's next work on fungi is contained in his *Flora*

* This volume was never published. There are sets of the sixty plates in the Society's library (sent to J. E. Smith by O. Targioni Tozzetti) and in the British Museum (Banksian) library (obtained at Lord Bute's sale, 1794), with the title '*Icones Plantarum submarinarum*'. Three of these plates are published in G. Targioni Tozzetti's posthumous *Catalogus Vegetabilium marinarum* (1826). G. Targioni Tozzetti, however, completed and published Micheli's *Catalogus Plantarum Horti Caesaris Florentini* in 1748. There is a copy of *Nova Genera Plantarum* in the British Museum which belonged successively to the three generations of Targioni Tozzetti—Giovanni, Ottaviano and Antonio. Most of the original drawings are inserted opposite the plates.

† A. von Haller, *Enumeratio methodica stirpium Helvetiae indigenarum*, 1742.

‡ *Peziza sordide alba acetabulis ellipticis imperfectis*. [*Discina venosa*.]

§ *Clathroides, flavescens pediculo carens*. [*Trichia favoginea* Pers.]

|| J. J. Dillenius, *Catalogus Plantarum circa Gissam sponte nascentium*, 1718. The drawings of fungi, lost since 1747, were recently acquired by the Department of Botany (British Museum).

Suecica, 1745. He lists ninety-eight species; but *Gymno-sporangium*, *Hirneola* and *Coryne* are placed in the algae in the genus *Tremella*. Here again there is a competent treatment of the subject, with occasional notes.

Fungi receive scant notice in *Philosophia Botanica*, 1751. There are no important references to them except 'The order of Fungi is still Chaos, a scandal to art, no botanist knowing what is a Species and what a Variety' *.

Species Plantarum, 1753, so important for its influence on the study of flowering plants, had no importance for that of fungi except that it applied the binary system of nomenclature. Ten genera are given—*Agaricus*, *Boletus*, *Hydnum*, *Phallus*, *Clathrus*, *Elvela*, *Peziza*, *Clavaria*, *Lycoperdon* and *Mucor*—*Byssus* being removed to the algae, but containing only one fungus, *B. phosphorea* [*Corticium caeruleum*]. Counting three fungi in *Tremella* in addition, there are only ninety-two species treated as against over 1020 in Micheli's *Nova Genera Plantarum*. It is remarkable that there are less fungi listed than in *Flora Suecica* mainly owing to the fewer species of *Agaricus*; in this genus he again refers to the lack of herbarium material. The same ninety-two species are listed in the tenth edition of *Systema Naturae*, 1759.

The lack of dried specimens is well seen in Linnaeus's own herbarium. At present it contains only 105 specimens of fungi. Of these only ten were written up by Linnaeus; ten have the handwriting of F. Ehrhart.

Beyond the application of the binary system of nomenclature to fungi in common with other plants and animals, Linnaeus thus had little or no influence on mycological systematy; his apparent waywardness in the employment of classical names was of less consequence here than elsewhere because the genera were so few. He instituted the class Cryptogamia for fungi and other groups without flowers, believing that all organisms had sex but that in certain of them this was not apparent †.

Linnaeus, however, greatly affected the course of the study of the group by the support he gave to the ideas of Baron Münchhausen—Otto von Münchhausen‡, not the Baron§ whose exploits were testified to by Gulliver, Sinbad and Aladdin. Münchhausen published in his periodical *Der*

* 'Fungorum ordo in opprobrium artis etiamnum Chaos est, nescientibus Botanicis in his, quid Species, quid Varietas sit.' (p. 241).

† In *Species Plantarum*, *Lycopodium* is included in Musci: liverworts, lichens, *Chara* and sponges are included in Algae.

‡ The genus *Munchausia* Linn., Mantissa, 243 (1767) was founded on a Chinese species described by Münchhausen.

§ These were written by R. E. Raspe, scholar and rogue (at one time Hon. F.R.S.) based on printed accounts of tales told by K. F. H. Baron von Münchhausen (1720-97) in the neighbourhood of Hannover. The original edition, though having the imprint 'London', was printed at Göttingen.

Hausvater, 1766*, accounts of the germination of spores. 'Fungi, when they become old, and especially *Lycoperda*, and all moulds, scatter a blackish dust; if this is observed under a good magnifying glass we find semi-transparent, not dissimilar spheres filled with black points inside, of the substance of a polyp. I have kept such dust in water and at a moderate temperature, when the spheres swelled up and changed into oval, mobile, animal-like balls. These little animals (at any rate I will call them so because of their resemblance) move about in the water; and when one observes them further the next day they form clumps of hard web and from these arise moulds or fungi. Where fungi grow, at first one sees white veins which one regards as roots but which in fact are nothing else than tubes in which the polyps move back and forth and which soon form a large structure'. He further states that the tissue of toadstools, especially 'Zunder' (amadou) is similar to that of polyps. He has no doubt that all corals, fungi, moulds, lichens, smut in corn, indeed probably all fermentation have their origin from small animals similar to those forming polyps: he does not regard these as complete animals, but promises further grounds for his belief following extended study. He believes that all terrestrial fungi and lichens are, like marine lithophytes, formed by polyps. Two years later he states that the spores of toadstools are the eggs of small animals and that the fungous fruit-body should not be regarded as a plant but as the dwelling and edifice of innumerable small animals. He adds that Linnaeus has written to him confirming the results and will soon publish his account 'ein so grosser und fleissiger Naturforscher wird diese zweifelhafte Materie am besten in ein helleres Licht setzen, und hoffentlich mehrere Naturforscher zu neuen Versuchen aufmuntern'.

This was a period when many were examining infusions of pepper, hemp and other vegetable seeds with their microscopes. Münchhausen had corresponded with Linnaeus, who eventually became stimulated to undertake investigations on fungus spores†. Writing to the Swedish mathematician

* 'Der Hausvater' first appeared in 1765 and continued till 1774 (vol. vi.); some parts were reprinted. The title was occasionally given as 'Des Hausvaters'. Originally it was anonymous.

† According to E. Ährling's *Carl von Linné's Briefwechsel* (1885) there are seventeen letters from Münchhausen in the Linnaean Correspondence.

Owing to the moving of this from Burlington House it was not possible to consult it without a derangement which appeared unwarranted. Fortunately there are copies of the letters at Uppsala, and during the printing of this address Dr. A. Uggla, Secretary of the Swedish Linnean Society, has most kindly abstracted from them the references to cryptogams, and from any replies of Linnaeus of which there are copies. (See p. 364.)

Wargentin, in October 1766, he says that for ten years no one took any notice of Münchhausen's discoveries, but recently he had observed Smuts and fungi develop in water, seeing movements like those of fish in lakes. Finally these little worms became immobile and eventually changed into fungi—a wonderful metamorphosis. How actually the worms moved he could not ascertain. They did not swim like fish or eels or fly maggots, so they may have some invisible organs for movement at the front end of the body.

Linnaeus had the problem made the subject of a thesis by his pupil J. C. Roos, which he presided over in March 1767. In the thesis, *Mundus invisibilis*, the candidate states that Nob. D. Praeses (i.e. Linnaeus) had recently been examining the seeds of *Ustilago* and had shown him very bright bodies arising from them, moving and running up and down in the water like fishes. They were truly animal-like and afterwards became quiet and stationary—unbelievable if not seen*. The full problem set Roos was the study of the invisible world as revealed by the microscope, and the thesis is mainly a general summary of the observations recorded by the early microscopists. The realm of nature is an immense museum; the large theatres are open to everyone, but the innumerable small rooms are locked and can be entered only by those possessing the key. The immortal Münchhausen had dared to enter a door before which many had stood with hair erect and spirit stunned, desiring to explore the treasures in the room. This inestimable author had written to Linnaeus ten years previously ('ante decennium') describing his experiments with *Ustilago Hordei*. Two of Münchhausen's published notes are given in full; indeed the whole of Münchhausen's writings on the subject occupy only about half a dozen small octavo pages.

The original observations in the thesis are very meagre, and are mostly a repetition of what is contained in Linnaeus's letter to Wargentin. The animalcula from *Ustilago* spores are described as oblong with a more obtuse anterior end, and it is suggested that movement may be due to a mechanism similar to that of *Volvox*. The observations were made with a Cuff's microscope. It is obvious that Linnaeus regarded Münchhausen's observations as of the very highest importance. Even allowing for the text being in Latin, one is struck by the manner in which Münchhausen is referred to—there is always some flattering adjective; the immortal glory of the discovery belongs to the illustrious author.

* 'Lege naturae hucusque inaudita & intellectum hominis omnem superante, ut fieri non posse dicerent multi, nisi videre oculis & palpare manibus rem liceret.'

As we should expect the fundamental question is faced, Are fungi to be referred to the vegetable or to the animal kingdom? or should they form a new natural kingdom which should be called neuter or chaotic? Should Polyyps, Infusoria and fermentatives be referred there? *.

Fungi certainly differ very much from other plants, they seem also to be distinct from animals; might not their place be 'inter regnum animale & vegetabile'.

Here we see the explanation of what has puzzled some of Linnaeus's commentators—the genus *Chaos* of the twelfth edition of *Systema Naturae* published in the same year. Linnaeus believed that he was dealing with facts, and he attempted to classify his data. He was confused undoubtedly, for he appears not to distinguish between fungi as such and the animalcula which arose from their spores. His *chaotica* were fungi when first mentioned, but in the *Scholia* † at the end of the thesis we find they are animalcula ('Anne minima ista animacula, *chaotica* dicta, mere medullaria, corporeque organico fere destituta sint').

The genus *Chaos* grouped under Vermes is defined as having a free body, uniform, reviving and with no external joints or sense-organs. There are six species:—*C. redivivum*, *C. Protheus*, *C. Fungorum*, *C. Ustilago*, *C. infusorium* and *C. obscurae*. *Chaos Fungorum* is apparently the mobile organism which arises from the spores of *Lycoperdon*, *Agaricus*, *Boletus*, *Mucor* and the remaining fungi; it is the metamorphosis of zoophytes from vegetable to animal, and, on the contrary, that of fungi is from animal into vegetable. *C. Ustilago* is apparently the spores of Smut on barley, wheat, and other Gramineae and *Tragopogon* and *Scorzonera*; the 'germination' is described by microscopists from various infusions: it is queried whether it is sufficiently distinct from '*C. Fungorum*: *Mucoris*?' The last species, *C. obscurae*, is rightly named; it includes six varieties, all with a query ‡.

* 'Quaestio inde oritur, utrum Fungi ad *vegetabilia*, an vero ad *animalia* refferri debeant? vel etiam an novum formari debeat regnum naturae, quod neutrum seu *chaoticum* vocetur? An Polypi huc referendi? An Moleculae vivae, *animalia infusoria* dicta, huc trahendae? atque hoc ad ipsum fermentum seu putredinem prope accedit.'

† The first two of these are (1) Why do fungi appear in autumn? (2) Why does *Mucor septicus* destroy house timber in certain places? Presumably this refers to the dry rot fungus *Merulius lacrymans*. *Mucor septicus* of *Species Plantarum* is *Fuligo* (*Mucilago*).

‡ α Februm exanthematicarum contagium?

β Februm exacerbantium caussa?

γ Siphilitidis virus humidum?

δ Spermatici vermiculi Leuwenh.?

ε Aethereus nimbus mense floescentiae suspensus?

ζ Fermenti putredinisque septicum Munch.?

Many living molecules, which perhaps belong to this family, lie hidden to be revealed by posterity.

It is difficult to understand why Linnaeus should have made such a lamentable lapse in the last edition of his great *Systema*. As a microscopist he was certainly not to be compared with most of those whose work he treated in a seemingly casual manner, but his point of view cannot properly be understood without a consideration of *Mundus invisibilis*. So acute in his sense of affinities, so sure-footed in so many different fields, Linnaeus here came sadly to grief. 'Deus creavit, Linnaeus disposuit'—but in this instance, confused by his belief in the value of Münchhausen's observations on the polymorphy of fungi, in attempting to classify what he didn't understand he took a great step backwards.

From a footnote* in the collected editions of the *Amoenitates*, 1767, it seems that Linnaeus is becoming a little uncertain. He compares the appearance of the little worms arising from the fungus spores to infusoria, and says how impossible it is without exact experiments to be certain whether they become fungi.

In the Linnaean correspondence for the years 1767 and 1768 there are several letters between Linnaeus and John Ellis—the most candid and friendly of Men—which suggest why Linnaeus became a little open-minded on the question.

Linnaeus to Ellis.

Jan. 1, 1767.

With regard to *Fungi*, you may pick up, in most barns or stacks of corn, spikes of wheat or barley, full of black powder, which we call *ustilago*, or smut. Shake out some of this powder, and put it into tepid water, about the warmth of a pond in summer, for three or four days. This water, though pellucid, when examined in a concave glass under your own microscope, will be found to contain thousands of little worms. These ought first to be observed, to prevent ocular deception. In mould, *Mucor*, you will find the same, but not so easily as in the larger *Fungi*. If, in the course of from 8 to 14 days, the water has been kept up to the same temperature, you may observe how these minute worm-like bodies become fixed, one after the other, and acquire roots. I have just printed a dissertation on the Invisible World, which shall be sent you by the first opportunity. These chaotic worms are nearly akin to the last species of animals which I have placed in my *Systema*, under the genus *Chaos*.

Ellis to Linnaeus.

Sept. 8, 1767.

I have lately been trying experiments on the seeds of the Fungus, called by you *Agaricus campestris*; and also on those called the *Agaricus fimetarius*. The minuteness of these bodies, obliged me to make use of the first magnifying glasses in the double microscope. This plainly

* 'Vermiculi hi simillimi sunt vermiculis infusoriis, ut primo dubitabam, utrum essent specie distincti, aut etiam mere infusorii multiplicati, cum non licebat mihi continuare experimentum, usque dum in fungos enacerentur.'

shewed to me, that these seeds, though put into water according to your directions, have no animal life of their own, and are only moved about by the *animalcula infusoria*, which give them such a variety of directions, both circular, as well as backward and forward, that they appear as if alive.

The *animalcula* are so numerous, and at the same time so pellucid, that without good glasses the most accurate observer may be mistaken. I wait for an opportunity to try the seeds of the *Lycoperda*, and the dust of the *Ustilago* in corn.

Linnaeus to Ellis.

Oct. 1767.

I received yours, in which you speak of the living seeds of *Fungi*, asserting that you have only seen the *animalcula infusoria*, moving the powder of these vegetables.

I am not able rightly to understand whether you have actually seen the *animalcula* or not. If really so, they ought, at the end of 14 days, to begin to attach themselves to the bottom of the glass, first a solitary one, then several more adjoining to it, till almost all of them are thus become fixed; after which they grow up into *Fungi*.

With respect to the *animalcula infusoria* themselves, unless I am totally mistaken, I think I have seen these to be the living seeds of Mould, *Mucor*. But before I venture to put forth such an opinion, I beg of you to lend me your lynx-like eyes; and you will see in the vessel or glass, where there is so little water that it may soon evaporate, whether these bodies do not change to plants of *Mucor*. This point is of the greatest importance, and if my ideas be correct, we shall no longer be surprized at the quantity of such *animalcula* in common water, any more than at the mould itself on decaying food, etc. I beg and intreat of you not to slight my request. You will find it worth your while to look closely into the nature of these minute beings, as they are related, though remotely, to your own marine *animalcula*. Every body wonders at the *animalcula infusoria* being produced by an infusion of pepper, and such substances; whereas the difficulty vanishes if they belong to *Mucor*; for pepper if long kept moist, is as liable to grow mouldy as any thing else.

Having once discovered the little worms in the *Ustilago*, by the help of the microscope, I can now see them with my naked eyes, though less distinctly; and I showed them a fortnight ago to some of my pupils.

Ellis to Linnaeus.

Oct. 30, 1767.

I have received your obliging letter about the seeds of *Fungi* being animated. By your letter, you seem to think, that the seeds of the *Fungi* are animated, or have animal life, and move about; my experiments convince me of the contrary. I must first let you know, that I am convinced that in almost all standing, or even river, water, there are the eggs, and often the perfect animals, of those you call *animalcula infusoria*. As soon as these meet with their proper *pabulum*, they grow and increase in numbers, equal to the *Musca vomitoria*. I often have examined river water and pond water, and scarce ever found it without some species of these *animalcula*, especially in summer and autumn: besides, the same *animalcula* that attack, eat, and move about the *farina*, or seeds of the *Fungi*, do the same with other vegetables, as I have lately been convinced of by a fair experiment. I have tried at your request my experiments over again, and shewed them to D. C. Solander. I will keep these infusions according to your desire 14 days, and examine the particulars you desire of the *animalcula* fixing themselves, first one, then many more, to the bottom of the glass; and will endeavour

to find out what you mean by their 'growing up into Fungi'. If you mean that *animalia infusoria*, when they are dead, are a proper *pabulum* for *Mucor*, I agree with you; for I have many animal substances that are covered with *Mucor*, even between the Muscovy Tales (or *Glacies Mariae*) used on purpose for microscopic animals, in the microscope. But what appears to me most difficult to comprehend is, for instance, I have now a *Lycoperdon Bovista*, which I received from our good friend P. Collinson four days ago. I put part of it into river water, and in two days' time I perceived the seeds or *farina* of it moving about distinctly. The fourth day I perceived the figure of the *animalcula* that moved them. Are these seeds, or these *animalcula*, (for they are evidently distinct bodies), to turn into *Fungi*, *Mucores*, or *Lycoperda*? This is what I do not comprehend in this new discovery. If the *animalcula*, that moved the seeds of the *Lycoperdon*, it would be amazing; and again, it would be as surprising that the seeds of one genus should produce another; for instance, that the seeds of *Lycoperda* should produce *Mucores*. However, I have determined to go through these experiments with precision, and to call in witnesses of the several appearances.

I have not yet got any of the *Ustilago*. If you will be so good as to send me a Spike of Corn infected with it, proper for trial, you may depend on me in carefully going through the experiments properly.

Linnaeus to Ellis.

Dec. 8, 1767.

I am beyond measure delighted with your observations upon the *Lycoperdon* in river water; that its powder moved about, and was transformed into that species of *Mucor* which I have named *Mucedo*. I have long suspected this *Mucedo* to belong to *Lycoperdon*; but my suspicion has never before been confirmed.

Ellis to Linnaeus.

Jan. 15, 1768.

In your letter of the 8th December, you seem to misapprehend the meaning of the letter which I wrote to you the 30th October. I find, on looking over the copy which I have of it, it runs thus, or much to this purpose:—

[Then follows an account of his experiment with the spores of the giant puff-ball.]

Thus far I thought it necessary to quote from my former letter of 30th October, as my real opinion. I have kept a regular journal of my observations in making my experiments on the seeds of the *Fungi*, which I have shewn often to Dr. Solander, to prevent any mistake; and do assure you I have convinced him that they do not move of themselves when kept in water; but it appeared evidently to him, and many more gentlemen who saw my experiments, that the motion which they had, proceeded from *animalia infusoria*, whose shape we plainly saw, and observed distinctly the particular motion, with some attention, which these little creatures had while they were eating the seeds of the *Fungi*, and which they communicated to the seeds of the *Fungi*, so as to make them appear alive.

Ellis to Linnaeus.

March 15, 1768.

I have now discovered why putrid vegetable substances yield volatile alkaline salts, the same as animal substances. I put a rotten potatoe into water, about ten days ago, in a glass, and covered the top with a card, having a weight on it to keep it close, and placed it on a shelf

in a room over the fire-place. In four days the water was full of small animalcules, so that, I believe, for every particle of the potatoe there were ten minute animals, as in the experiment with the *Fungi*. In order to know for certain whether these animals came from the potatoe or the water, I boiled a small potatoe till it was ready to fall to pieces. I likewise boiled some water for half an hour, and then put the mashed potatoe and the boiled water together in a glass, and they were placed in the same warm situation, with a card over it. I examined a drop of the liquor four days after, and could perceive millions of animalcules, of a tadpole shape, turning about the crystalline round particles of the potatoe in all directions, just as I had observed them turning the seeds of the *Fungi* last autumn. I must inform you I used the largest magnifiers I had, which were the first and second of Wilson's microscope. I wish you would try the same experiments; you will find many new scenes in nature will be discovered by this hint. I have showed the experiment to Solander and a very few friends, but have not yet made it public.

I wish Baron Munchausen would try the same.

It is probable that if Linnaeus had not supported Münchhausen's views little or nothing further would have been heard of them. The periodical in which they were published was not widely distributed, and the few odd notes in it would doubtless have been disregarded but for the lavish praise Linnaeus showered upon their author. Linnaeus at that time was at the height of his reputation and few, if any, disputed his authority in the realm of natural history*. The result was as Münchhausen had foreseen, for immediately, fungi—

Nomades, auctumnales, barbari, denudati, putridi, furaces, voraces. Hi flora reducente plantas hymenatum, legum relictas earum quisquiliis sordesque †—proving unamenable to the Linnaean discipline, attracted many investigators, and not a few impostors. It was only to be expected that there should be efforts to wrest the pride of priority from Münchhausen.

John Ellis, whose notes and sketches are one of the treasures of our Society, followed up the investigation he had carried out at the request of Linnaeus—as he says, ‘the satisfaction I have received from clearing up this point led me into many other curious and interesting experiments. The result was the same.’ Ellis convinced himself that the spores of fungi, like the seeds of flowering plants, are unrelated to the animalcules which appear when they are placed in water. In order to prevent the extraordinary doctrine of the Baron's from spreading in this kingdom he published immediately an

* ‘Un sentiment que M. Linnaeus appuie, est pour moi presque une vérité.’ J. E. Guettard, *Mémoires*, II 473 (1770).

† ‘I doubt you will conceive that Linnaeus has gone mad, if I tell you his opinion concerning *Funguses* . . . What Linnaeus means, I do not at present understand; but the very dreams of so great a genius merit our attention.’ Thomas Martyn in letter to Richard Pulteney, Feb. 18th 1767. G. C. Gorham, ‘Memoirs etc.’ p. 134 (1830).

† *Syst. Nat.* Ed. 12, p. iv.

account of his experiments in the 'St. James's Chronicle' 22 September 1767.

One Georg Wilk, said to be an Englishman, but of whom I can find no details*, published in the 'Staats- und Gelehrte Zeitung des Hamburgischen Correspondenten', 1768, an account of how he took the pellicle from below a mushroom and moistened it: some minutes afterwards the water was coloured red. A drop was placed under a Wilson's microscope, and showed round red semi-transparent globules which he regarded as seed, in each of which was a blackish spot. The pellicle was kept in water and on the third day slight movement was apparent in the globules, becoming more obvious and circular the following day. Wilk concluded that the mushroom seeds were animalcules, they moved like tadpoles or small eels with incredible liveliness. He saw them mass together and push out tender fibrils representing roots. In the same water, especially towards the bottom, there were larger animalcules, resembling those which in summer occur in water in which flowers or plants have been kept. He regarded fungi as plants, though he appreciated the difficulties in doing so in view of his results†.

* It is not without interest that the celebrated physicist Johan Carl Wilcke, Secretary of the Swedish Academy and brother of Linnaeus's pupil H. C. D. Willeke (respondent of the thesis *De politica Naturae*), occupied his free evenings in microscopy, with a view to examining Needham's assertion that certain microscopic plants and animals were reproduced without eggs and wrote two short papers, one in 1761 on aquatic insects, the other, in 1764, on some small plants which grew in drinking glasses.

It would be tempting to identify Wilcke (Wilke in the German edition of the Swedish Academy's Transactions) with Wilk, but in addition to the difference in initials there is the fact that Wilk describes himself as 'weder ein Naturkündiger, noch ein Gelehrter, noch von sich selbst eingenommen'. Further the former used Cuff's¹ microscope—the property of the Academy—whereas the latter used Wilson's².

† R. Pickering had made a much sounder observation in 1744 though drawing from it a wrong conclusion. 'Upon Examination of several Mushrooms, exposed to the open Air, but kept from the Injuries of the Sun and Rain, I find no *Animalcula* bred therein, nor, as yet, a Tendency to Putrefaction; though they have been exposed thus for a Week. On the other hand, upon examining a Mushroom, very far from being full-grown, putrefy'd by the Rain, and Moisture of the Dung in the Bed, I found *Animalcula*, discoverable only by the third Magnifier, floating in the Liquor, squeezed out from it: From which I think it evident, that the dangerous Consequences which History has informed us to have attended the Eating of Mushrooms, have not arose from any poisonous Quality essential to them, but from the accidental *Ova* or *Animalcula*, which the Richness of their Nutriment has allured to them, and which their Contiguity to the Ground, and the Places they are produced in, render them obnoxious to.'

¹ John Cuff, Description of a Pocket Microscope, etc. (1743); The description of a new constructed double microscope (1744).

² James Wilson, The description and manner of Using a late Invented set of small Pocket-Microscopes &c. (1702).

F. G. Weis (later Weiss) in his thesis 'Plantae Cryptogamicae Flora Gottingensis', 1769, gives the credit of the discovery to his former professor, D. S. A. Büttner, who had described two experiments to him apparently both privately and in lectures, but published nothing on the subject. The story told is that in 1756 Büttner collected some toadstools for the purpose of enquiring into their nature and qualities. They were placed separately in the windows of a room and left; they gradually became rotten and gave off a white powder. This powder when examined with a microscope was found to consist of innumerable very small pellucid globules, like eggs, which broke with a slight noise when pressed with the finger, and suddenly gave forth a limpid material. The globules, after some time, became converted into pupae and then into innumerable flies, the species of fly differing according to the kind of toadstool. No further experiment could be carried out, for domestic reasons, until 1760, when similar results were obtained. In 1751 he had examined *Cyathrus* and decided that the periodiola are not true seeds; his ideas about the structure of toadstools correspond closely with those of Münchhausen.

Care is taken to give such unessential details as that he exposed the fungi in the first experiment 'chartae coeruleae superinstructos' and that those in the second were carried in a wooden box, but it is thought sufficient to have examined putrid remains of toadstools to found a school of thought and claim priority. It is certain that Büttner did not see any spore-deposit on his coloured paper and that the globules of white powder he looked at were something other than spores. If he had cut open the toadstools when he gathered them he would doubtless have found fly maggots—indeed, some species as e.g. *Amanita rubescens* are almost invariably maggoty. Weis's thesis formed the introduction and the first thirty-five pages of his full work published the following year and dedicated to G. A. L. B. de Münchhausen. He unhesitatingly removed fungi from the vegetable kingdom giving several reasons for so doing, all of them wrong. He states that if fungi were true plants the principal parts such as fruits and seeds would not be entirely lacking; the extremely rapid development in a night by which fungi often acquire a surprising size is not a plant quality; annual plants do not perish without leaving seeds, bulbs, or other parts to carry on in the same place and their death is by drying, whereas fungi either rot completely or, if they dry, leave no part which can carry on in the same place, for they do not grow in the same spot in successive years. Weis was an excellent cryptogamist, but he obviously had little knowledge of field mycology; he based his last statement on information by country people who gathered morels.

J. Beckmann sent a copy of Weis's thesis to Linnaeus saying he thought he would be amused at Büttner's observations on the change of fungus seeds into insects. Presumably Beckmann knew of Münchhausen's work, for he had written to Linnaeus in 1766 asking him to commend him to O. von Münchhausen 'qui mihi a Te admonitus facile locum inter professores Goettingenses comparabit'. He adds that it is not, however, he but his relative G. A. Münchhausen 'qui in patria mea clavum imperii tenet'. ('Jam Tibi dissertationem juvenis, qui Botanicam, Bütnero doctore, magno studio coluit, mitto, quam ut gratioso vultu accipias, auctoris ipsius verbis rogo. Ridebis haud dubie absonam Bütneri observationem de mutatis Fungorum seminibus in insecta. Scilicet Bütnerus zoologia non erat imbutus.') Linnaeus replied immediately about the thesis that he hoped the whole book would soon be published, because it threw so much light on the most obscure class of cryptogams ('utinam me vivo ederet totum opus, quod maxime illustraret obscurissimam hanc familiam').

Opinions about Büttner differ. Medicus said he had the unusual fault of knowing much and writing little. It may be of significance, as W. J. Lütjeharms has pointed out, that Büttner's pupils, J. P. Rühling (1766) and P. D. Giseke (1767), both omitted fungi from their theses on plant classification. Rühling included *Mucor*, but he regarded it as an alga: Giseke says 'Fungi e regno vegetabili ad animale videntur obligandi'. (It was the same Giseke who was afterwards a pupil of Linnaeus.) On the other hand, this was not the first claim to priority that Büttner made, though he went further than as he stated that his results had been stolen*.

* John Ellis had published 'An Essay towards a Natural History of the Corallines' in 1750. P. Ascanius, the Danish Botanist, wrote to Linnaeus from London in 1755 'Mr. Ellis, F.R.S., has just published a treatise on Corallines, *Sertulariae*, which, by means of an excellent microscope, he has discovered to be entirely the work and crusts of Poly pes, by which they are inhabited throughout their whole length. . . . The original author of these experiments is Dr. Buttner, who has lately left Paris for Berlin'. Ellis did not hear of the claim until 1765, when he wrote to Linnaeus. 'About a month ago . . . I was shewn a printed book of the Lives of the Professors at Gottingen in Germany. [J. S. Pütter, Versuch einer academischen Gelehrten-Geschichte von der Georg-Augustus Universität zu Göttingen, 1765.] Among the rest, to my astonishment, I saw that Professor Buttner has had the assurance to write, or give the following account of himself, relating to my discoveries of Corallines. He says, "besides a considerable number of sea plants, he discovered also the manner of generation of many habitations of Poly pes, taken for plants. These discoveries he laid, 1750, at London, after a voyage thither, before the Society of Sciences there; when John Ellis from Ireland, a member of it, communicated them afterwards to the world, under the title of an Essay towards Corallines, with copper-plates, which he got done at his own expence, besides some additions of his own"'. Ellis had met Büttner in London, but most solemnly declared to Linnaeus that he had never received any information

Meanwhile, O. F. Müller in 1768 had described the development of what he considered to be a new race of animal-plants. The organism was *Pilobolus crystallinus* occurring on horse droppings. *Pilobolus* was first described from Virginia in Ray's 'Historia Plantarum', 1688, and H. Baker in 1743 gave a good description of a species he found on a culture of black mud from the Thames. Müller had found the fungus in 1764. Touching it with his fingers he felt a movement, and heard a slight noise as if something had broken: probably he heard the sound made when the sporangium is projected. He gives a good description of his 'Kristallschwämmchen' describes the formation of the sporangium and recognizes the 'seeds'. In many of the club-shaped sporangiophores he saw very slender white worms which he describes as swimming here and there in a small ocean. 'What shall we think of these phenomena? A kind of plant which changes into a small crystalline club enclosing a living worm, and a few hours after that becoming transformed into a fungus; in the morning transparent, in the afternoon a darker body; a small animal, which has a very bright residence, which swims in the clearest moisture, and in a moment becomes enveloped in a dense cloud and closed in a thick body.' He decides that the worm could not have entered from without because there was no break in the club; and the structure obviously was not a gall—the worm having prepared its own grave. He does, however, query whether the worm was present in the horse-dung and developed at the same time as the club-shaped structure. Naturally the question is asked what these 'kristallinische Körperchen' are to be named and in which natural kingdom they are to be placed. The three kingdoms have obviously too restricted boundaries to enclose it and many genera of polyps and infusoria.

from him on the nature of the animals, 'for he never went with me to the sea side, nor never saw them (I really believe) till he saw the figures of them in my plates . . . only botany was our conversation when we met'. In the Introduction to his Essay Ellis says 'In order to preserve some Specimens of the most rare Kinds . . . I expanded them on Paper in fresh Water, laying out their fine Ramifications with some Exactness; for which Method, with many useful Hints in Botany, I am indebted to that excellent Botanist Mr. Büttner, of Berlin'. This probably means no more than what it implies, i.e. that Büttner had a method of mounting 'sea-plants'. Ellis's note books give conclusive proofs of his observations; a certificate from the Secretaries of the Royal Society that Büttner 'did not give in any paper to the Society relating to corallines, or any of those marine bodies which he says he did' seems equally conclusive. Linnaeus had obviously heard much to Büttner's discredit 'He, poor man, destitute of any discoveries of his own, tries to steal that celebrity. . . . I shall write to Baron Munchausen about Büttner's ill behaviour'. Ellis also wrote to Munchausen, and so we come full circle.

In 1769 Ellis again referred to Münchhausen's doctrine in a paper read before the Royal Society. His opinion is seen clearly in a letter published in the 'Gentleman's Magazine' for 1773. The Rev. Richard Watson, M.A., F.R.S., had written in 'An Essay on the Subject of Chemistry'—'It is not yet clearly decided amongst naturalists, whether the seeds of mushrooms, of mucors, and of the whole class of fungi, be not, in a tepid, humid matrix, changed into vermicular animals, which lose in a little time their power of spontaneous motion, coalesce together, and grow up into those very singular plants: the quickness of their increase, and the irresistible force with which the least mouldiness propagates itself, and destroys the texture of the bodies upon which it fixes, seem to point towards an animal nature', and apparently Ellis took occasion to write strongly to the Royal Society about the matter. The covering letter to the 'Gentleman's Magazine' reads: 'The following letter was sent to the Royal Society to prevent the growth of an absurd, unnatural doctrine, exactly similar to the Romish doctrine of transubstantiation, and which has lately been assented to by an ingenious gentleman of Cambridge. It was, I hear, refused being printed in the Transactions on this account; but, as truth ought always to be supported when proved by repeated experiments and before competent judges, I think it not unfair to lay it before the public for their impartial judgment'.

'To Doctor Matthew Maty, Secretary to the Royal Society.

When men of eminence introduce a new discovery as the result of experiment, the generality of mankind are too apt to receive it implicitly for a fact, without giving themselves the trouble of *repeating* the same *experiments* to confirm the truth of their assertions. It is this want of attention that has occasioned some ridiculous absurdities to pass upon the world for surprizing discoveries in the properties of animal and vegetable bodies, which nobody ever thought of before.

The illustrious Baron *Munckhausen's* new doctrine of *vegetables changing into animals*, and then into *vegetables* again, is of this kind: and, tho' it must be allowed to be contrary to the course of Nature, yet the Baron's credit gained it advocates; even the celebrated *Linnaeus* adopted it upon receiving an account of it in the Baron's letter, depending on the *truth* and *accuracy* of the author's own experiments without examination'. Ellis refers to the 'remarkable lines' in *Linnaeus's 'Systema',—*

'Zoophytorum metamorphosis e vegetabili in animale
Fungorum itaque contrario, ex animali in vegetabile',

and ends 'But I hope I shall soon be able to clear up to the

world the absurdity of the first as much to my satisfaction as I have done that of the last'.

The ball, however, had been set rolling and numerous articles were written. Some of these were very short, but received remarkable attention; it is usually more difficult to trace them than to learn of their existence. Those who did not themselves make observations were in no wise deterred from joining in the controversies.

It is worth noting that it was at this period that discussion was taking place on the nature of zoophytes. Pliny had written of 'bodies which have a third nature, that of the animal and vegetable combined' and the name zoophyte is sufficient indication of the general belief in the view. Coral-ines were traditionally regarded as fossils or as stones, though it became known that they grow and produce fruits. Most thought them plants and some even fossil fungi. Peyssonnel held that the 'flowers' are insects which inhabit the coral, and Réaumur that the coral is an alga which forms a supporting structure from shells and sand; Pallas thought they might be worm shells. Later the work of Ellis and others showed that they were animals, though Basto continued to put forward similar views to those of Peyssonnel and, so late as 1770, Guettard could write 'Les Botanistes surtout, jaloux de ne pas perdre une si belle branche de leur domaine, ont constamment rangé tous ces corps parmi les plantes'. There were various opinions about the nature and formation of these organisms and occasionally they are referred to in discussions on the similarly problematic fungi.

Without considering odd statements such as those of J. Hill who, in one of the twenty-six notes he sent for publication in the 'Hamburgisches Magazin', 1753, said that probably in the end we should go so far as to prove that fungi and other organisms are the work of snails and beetles which find in them both shelter and nourishment, there is abundant evidence of the difficulty found in understanding their mode of growth, their structure, and their classification, both general and special. Thus J. A. Scopoli in the first edition of 'Flora Carniolica', 1760, has 'Classis I. Fungi', following Haller who regarded them as plants, whereas in the second edition, 1772, he has a special section 'Plantae Dubiae' for algae and fungi in his 'Classis XXIV. Cryptogamia'; in comparing some habits of genera of fungi with those of *Hydra* he says that the smell of putrefying fungi is similar to that of putrid flesh—a similarity frequently stressed by later writers. In his 'Plantae subterraneae', the same year, he comments on the protean shapes assumed by fungi in mines and asks where possibly seeds could have come from. In 1786 in describing *Lycoperdon arrizon* [*Pisolithus arenarius*] he complains that

there are so many innovations that no one will be able to find a way out of the fungal labyrinth. He is unable to decide whether fungi are plants or animals because the work of Linnaeus, Büttner, and Münchhausen has not been wholly refuted; if the production of a volatile alkaline salt on distillation is an animal character then *Lycoperdon* is an animal; the worms often met with in fungi, the cadaverous smell and the direction of the fibres, which differs from that of other vegetables, all support the view. He ends with a pathetic remark about what is left for posterity to discover:—
 'Quam multa adhuc latent, quae sera dies detegat.'

A thesis 'De generatio vegetabilium', 1773, with the names M. N. Leske* and E. S. Reiniger on the title page, deals with fungi in a section on cryptogams. Because it has been shown that fungi multiply by shedding spores 'non e regno vegetabili videantur ejiciendi'. It is conceded that fungi are the 'habitacula quasi insectulorum minimorum', but it is no more reasonable that they should therefore be regarded as zoophytes than, shall we say, that trees and herbs damaged by insect bites should be considered to be animals.

A second thesis, 'De dubia fungorum collectione', 1776, apparently presided over by G. R. Boehmer† (for though published in his name he ends by recommending G. S. Muller for his degree) after a description of the variation in fungi states that it is necessary to collect them 'in usum commodum'. Further, poisonous fungi often simulate edible ones, and these, moreover, often have deleterious effects because of the frequent presence of maggots in them. But if maggots inhabit fungi only by chance, and chiefly when they are old and becoming putrescent, can they be concerned in the origin of fungi? Fungi do not always contain maggots, but serve as food for them only in warm humid weather and when decaying. Wilk found two species infesting fungi. Cannot other species have a similar origin developing actively from eggs formerly existing there or coming from some other source?

The thesis of Jonas Dryander, 1776, our first honorary librarian and for many years a sort of permanent Vice-President, was on the vindication of retaining fungi in the vegetable kingdom:—*Fungos regno vegetabili vindicans*. It was presided over by E. G. Lidbeck of Lund, and was dedicated

* It is usually quoted as by Leske. The dedication is signed by Leske only, and his name is in slightly larger print on the title page; but both are given as 'Medicinae baccalaureus' and the plural is used throughout.

† The first of the corollaria to the thesis, 'De plantis in cultorum memoriam nominatis', 1770, by J. F. B. Breuel, presided over by Boehmer reads 'Fungi a recentioribus nonnullis haud bene a vegetabili ad animale amendantur regnum'.

to *avunculo optimo* Lars Montin, the pupil of Linnaeus who wrote to Dryander in 1783 asking him to try to persuade Banks to purchase the Linnaean herbarium and later, at the instance of C. P. Thunberg, to dissuade him from purchasing, or at least to leave the English collection acquired by the younger Linnaeus. It is headed with a quotation from Scopoli. 'Si fungos ac Lichenes animalia vocabis, quinam erunt limites inter duo Regna'. Obviously directed against Weis, the thesis takes circumstantial account of the points raised by various writers. In opposition to the view that because flies are present in fungi they must produce them, he points out that Linnaeus had listed a number of insects found on the same fungus. He considers that Münchhausen's results were of no theoretical consequence as O. F. Müller had shown that every organic body placed in water gives rise to animalcules and that these may be present even in fresh water. The arguments against the vegetable nature of fungi used by Weis are severally controverted, and thus the reasons for regarding fungi as animals were considered valueless. Further, experiments with spores must be examined with the greatest care because error is so easy with these very minute structures. Though Dryander does not record any personal observations, his thesis is well-reasoned and fundamentally sound.

Well-reasoned arguments, however, even if more widely circulated than in an out-of-the-way thesis, were not likely at this period to have much effect.

In another thesis, 'Primitiae Florae Holsaticae', 1780, by F. H. Wiggers*, presided over by J. C. Kerstens, the opposite view is taken. In the preface it is stated that fungi are by many regarded as doubtful members of the plant kingdom, but that in his opinion 'omnino ab hoc alieni sint'. He remarks upon their infinite variety and places them in an appendix in a group *Fungoideae*. (*Sphaeria*, however, is classed with *Fucus*, *Riccia* and *Blasia*.) Here he says they are of doubtful affinity, but are probably zoophytes constructed from vegetable remains as corals are from minerals or shells. He repeats many of the old arguments, but is influenced chiefly by Münchhausen.

In 1783 N. J. de Necker published his 'Traité sur la Mycologie'. This formed part of a mémoire sent to the Imperial Academy of Sciences, St. Petersburg, to compete for the

* It is well known that the candidate was G. H. Weber, who is referred to in the 'Praemonita'. The dedicatory page gives the pseudonym as 'Wickers'. In his 'Spicilegium Florae Goettingensis', 1778, Weber says that he had intended to add a section on fungi because the teaching of them laboured under the greatest difficulties; he had collected them and made notes on them, but too much remained to be done.

prize offered in 1779 *. Necker was unsuccessful and considered it his duty to publish the part concerning fungi because of the totally new discoveries: the remaining three sections demonstrating the non-existence of a sexual process in ferns, mosses, and algae, though publication was promised, never appeared. Necker's name is often mentioned in mycological text-books, because he is said to have recognized the mycelium as something distinct from the fruit-body, calling it *carcithium*. He defines this, however, as follows: *Le carcithe, Carcithium*, est la souche des champignons qui en doivent directement naître. La nature du carcithe, est dans son commencement, une fluidité apparente, à laquelle la solidité succède. . . . Le terme de Carcithe qui j'ai composé, dérive de $\kappa\alpha\tau\chi\epsilon\omicron\alpha\iota$ †, *initium facere*, faire le commencement . . . une souche organisée avec la dernière simplicité, qui est elle-même produite par une substance végétale devenue spongieuse ou réduite en terreau. . . . Cette même substance parenchymateuse ou cellulaire, entrant comme partie essentielle dans la compositions des végétaux, est très susceptible de modifications, en produisant des êtres fongueux de différentes formes'. This is in no way essentially different from Marsigli's views. Though his subtitle reads 'Discours historique sur les Champignons en général'—and it must be admitted that he gives a good account of the preceding twenty years—Necker nowhere refers to Marsigli, though he copies many of his illustrations. One of these figures the agarics which F. Bartolotius described as springing up in a flask which had contained *Nostoc* for seven months and therefore must have arisen without the presence of seeds because of fermentation: the letter is given in full with its title, but no clue where it is to be found ‡.

He himself regarded the powder of *Lycoperdon*, for example, 'comme un aggrégat de particules fort atténuées qui bien loin de faire naître la même sorte de champignon, elles ne fournissent qu'une apparence de croute de nature mucoreuse'. The Mucors which arise from the particles of fungi, can be regarded as a last effort of nature; they still possess some

* The subject was first set in 1764: *Per observationes, & experimenta explicare quomodo propagatio Plantarum, quae a Botanicis Classi Cryptogamicae annumerari solent, Filicum, Muscorum, Fungorum procedat?* and for a second time in 1779. The prize was one hundred ducats. It will be remembered that Linnaeus was the successful candidate for the prize in 1759.

† V. Picus in his *Melethemata inauguralia*, 1788, suggests that this should be $\alpha\chi\epsilon\omicron\theta\alpha\iota$. The thesis gives a detailed account of numerous writings on fungi. His conclusion is that the animal nature of fungi appears to be more than sufficiently proved.

‡ 'François Bartolotius, abbé italien, qui passoit dans le monde pour un personnage ingénu & défenseur de la vérité'—a pleasing touch which Necker must have delighted to write.

properties of the vegetable basis which is here reduced to its last term. Because, according to Necker, fungi are constructed on other models than are known in animals, plants and minerals, they should be excluded from these kingdoms. They should be considered as *mésymaux*, intermediate organisms. He proposed that they should form the third kingdom (*Regnum mesymale*) of nature between plants and minerals (which would become the fourth). In his statement he gives weight to some of the reasons put forward by Weis, but he rejects the Münchhausen doctrine and does not mention Linnaeus's suggestion of a fourth kingdom of nature to receive fungi. He brings forth the peeled onion to boil with fungi, so that its changing colour may detect the presence of poisonous kinds, which additional 'discovery' provides him with a resounding peroration.

R. Villemet (Willemet) * in an 'Essai sur l'histoire naturelle du champignon vulgaire', 1783 (1784) also independently suggested that fungi should form a new natural kingdom. He repeated Wilk's experiments at different times, places, and in different circumstances with the almost invariable result that he obtained insects and other small animals in fairly large numbers, sometimes so small that a microscope was necessary to see them. The essay covers a good deal of ground and ends in asking what should be done with this crowd of anomalous organisms which are of such amazing variety, having some vegetable qualities, a place in the zoological kingdom, and some sort of existence amongst minerals. He thinks the best plan would be to create a new class, and ventures to suggest its title as pseudo-zoo-litho-phytes. It would be subdivided into distinct species, the ordinary mushroom for example being described as a pseudo-phyte.

Villemet was led to his conclusions about the mineral affinities of fungi mainly by a consideration of the fungus-stone (*Pietra fungaja*, *Polyporus tuberaster*). The fungus-stone was known in ancient days only from Italy, mainly in the south and particularly in the region of Naples. It is a concretion of earth or tufa held together and permeated by fungus mycelium; when watered it produces an edible fungus, and does so repeatedly. Such an unusual phenomenon with its valuable economic possibilities was the source both of wonder and of various explanations. The first account seems to be that by Matthaeus Sylvaticus (d. 1342) in his 'Pandectes':

* Necker dedicated *Willmetia* (Compositae) to Villemet; his ideas on nomenclature were as confused as his mycological ones and by his system he bestowed unitary names generic in form on species, as my colleague Mr. J. E. Dandy pointed out to me.

'Lapis lynceis according to Evax *, arises from the urine of the lynx, coagulated on the top of mountains; this stone preserved indoors produces excellent mushrooms throughout the year; it furnishes a very useful remedy against dolores stomachis, icteritia, and fluxus ventris'. There are many references in older writers to a stone Lyncurium or Lyncaemum arising from the urine of the lynx †, but most of these refer probably to amber. However, this may be, there is apparently no mention of the fungus. But the commentators on Dioscorides, Pliny, and others knowing of the remarkable properties of the fungus-stone assumed that it was necessarily that to which such a strange origin had been attributed. It is mentioned by Hermolaus Barbarus (1516), Scaliger (1558), Caesalpinus (1583), Matthioli (1583), Porta (1588), C. Bauhin (1623), Parkinson (1640), Severino (1649), J. Bauhin (1651), Imperato (1695), Boccone (1697), Ray (1706), Marsigli, and Lancisi (1714), Micheli (1729), Battara (1755), Hill (1758), and many others. The first illustration is that by Boccone [Pl. 7, f]: Micheli showed that the 'stone' consists of earth, fragments of stone, wood, charcoal, or whatever may be present where the mycelium is growing. Goethe interested himself in the growth of the fungus-stone; Pepys desired a specimen; Sloane and Banks each obtained one. Berkeley states that he had 'seen specimens grown in England, in the nursery of Lee and Kennedy.'

J. F. Durande in 1785 describing 'le champignon ridé'—(*Polyporus lucidus*)—took the opportunity of criticizing Necker and Villemet, particularly the former. He says that, if fungi are due simply to the degeneration of plants, it is needless to propose a new natural kingdom for them. Both animal and plant kingdoms contain simple organisms, and just as the simplest insects belong to the animal kingdom, fungi must, in spite of the simplicity of their organization, belong to the vegetable kingdom. If our senses do not enable us to perceive their seeds ought we to assume that these are not present? The explosion of the 'mortier' of *Lycoperdon carpopolus* [*Sphaerobolus stellatus*] if not for the purpose of

* Evax, first century naturalist, about whom there is much uncertainty: he is reputed to have been an Arabian king. The manuscript of his 'De nominibus et virtutibus lapidum qui in artem medicinae recipiuntur' is at Oxford.

† Pliny has several references to statements by various authors, but regarded 'the whole of these statements as untrue'. 'Even those who maintain that it is not a variety of amber, still assure us that it is a precious stone. They assert, too, that it is a product of the urine of the lynx and of a kind of earth, the animal covering up the urine the moment it has voided it, from a jealousy that man should gain possession of it.'

dispersing seeds, nevertheless is an operation which is hardly consistent with an unorganized structure. Spores sometimes may not grow because of unsuitable conditions, and he points out that orchid seeds will not germinate: there are innumerable grains in the air which develop when the substratum and temperature are favourable. Putrefaction which destroys everything could never give rise to so regularly conformed, constant and uniform structures as, for example, *Sphaerobolus*. Fungi are better compared with mistletoe and other plant parasites. They are organized and living beings—in other words, they are true plants with a distinct place in the vegetable kingdom*.

It will be convenient to group the different opinions and beliefs so as to leave us free to follow the main course of development. There was usually an underlying philosophy, indeed frequently more philosophy than fact, but an attempt to trace the influence of one on the other would take us too far afield. Moreover, it is not possible to give more than a rough grouping, for obviously there is no clear dividing-line between the ideas prevalent at any one period.

It is not surprising that fungi played a part in the discussions on spontaneous generation which again came to the fore in the latter half of the eighteenth century. The story of the controversies on this subject both in its wider and its more restricted aspects has often been told. From Aristotle to Augustine, from Lucretius to Luther, the belief in spontaneous generation remained unshaken†. Eels, fishes, and frogs bred from mud bathed by sunlight, and a similar process perhaps explained the aboriginal Americans whose descent from Adam was difficult to trace. The theory in its crude form was demolished by F. Redi's experiments in 1668. With the advent of the microscope and the discovery of smaller and smaller organisms, the controversy was renewed—indeed, as microscopes improved, the centre of the discussion shifted until it reached the domain of biochemistry.

The results of Micheli's experiments on the growth of fungal spores were not received without much criticism. Many

* Durando quotes M. de Fontenelle, but I have not succeeded in tracing the original. 'Est-il concevable, que ces productions de la nature resultent d'un concours fortuit ou de quelques sucs diversément agités; que ce concours fortuit soit en même temps si régulier, qu'il produise toujours dans les mêmes especes une infinité de plantes parfaitement semblables; & si limité, malgré l'étendue infinie que le fortuit doit avoir, qu'il ne produise jamais aucune espece qui ait été jusques-là inconnue ?

† The second and fourth of the four books of Fortunio Liceti, *De spontaneo viventium ortu*, 1618, treat at length with fungi, including truffles.

thought that the 'seeds' were more like dust particles than true seeds and consequently were unable to accept his conclusions.

The first attempt to confirm Micheli's ideas came from his fellow countryman F. M. Mazzuoli, who in a letter to him which was not published until 1743 * gave the results of his experiments, which, however, he realized needed confirmation. He had bought some fungus-stones at Rome, and he questioned whether the sporophores growing from the stones were of the same nature as the stones (i.e. whether they were one species) or whether the stone served as substratum for any fungus. He put the stones in pots and covered them with earth from places where different species of fungi grew, and poured warm water on them. After some days fungi appeared in each pot, the species being the same as had grown in the places from which the soil was taken. He concluded that their seeds were present in the soil and these had been influenced to grow and produce sporophores because of the presence of the fungus-stone. By the aid of the stone it is therefore possible at any time to produce any given species: the stone acts as a 'formato', having the same effect as a fertilizer. To test this he allowed the spores of *Phallus impudicus* to fall into water which he then poured into the pots. After a time, five or six sporophores of *Phallus* appeared growing from the stones. He repeated the experiment with pieces of truffle, using the outside where he thought the spores were situated: the pieces multiplied.

It is most unlikely that Mazzuoli's results were sound, but it would be interesting, in view of modern work on factors influencing spore germination, to try the effect of the fungus-stone.

C. Seyffert in his 'De Fungis', 1744, which shows a sense of humour unusual in an inaugural thesis†, says that it seems contrary to reason that so ingeniously constructed a natural body as a fungus should arise spontaneously. Fungi contain variously anastomosing tubes and vessels having circulating nutrient juices. Moreover, they do not change their nature, but grow each year with the same appearance, new kinds being rarely observed. 'As for myself, I have observed between the gills of the *Amanitae* [i.e. *agarics*] a powder which the microscope shows as little lens-shaped bodies: this powder I have sprinkled on soil containing rotten wood, and the following year the same kind of fungus appeared there.'

* Micheli died in 1737.

† This was presided over by J. A. Wedel. The copy in the Department of Botany, British Museum, is a folio volume with 133 coloured drawings of fungi which have a title page '*Icones Fungorum quas ad vivam coloribus delineavit parens noster carissimus Henricus Christopherus Seyffertus.*'

J. G. Gleditsch in his 'Consideratio Epieriscos Siegesbeckianae'*, 1740, says that he can bear witness to the truth of Micheli's statements; he has seen the seeds of fungi and as far as possible has repeated his experiments. Moreover, the lowliest gardener knows that it is possible to cultivate Agarici, Boleti, Hydna, ect., if the caps are finely divided, carefully washed, and the water poured over the surface of fermenting dung; a copious supply of the same fungus appears after a short time showing that the seeds are the source of the growth.

In 1751 he published his results on the growing of moulds much on the lines of Micheli's experiments, but with modifications. He heated cylindrical vessels in an oven and while they were still warm placed pieces of melon in them and covered the opening with muslin. The vessels were put in various spots to provide different conditions; the pieces of melon became mouldy. He gives the details of the experiments. As the vessels had remained covered throughout he is convinced that spores must have entered through the muslin.

He remarked upon the astonishing smallness and prodigious numbers of these perfectly organized structures which reproduce their kind. They live in the air unseen, attach themselves to both living and dead plants, and enter our bodies through nose and mouth, and by everything we eat and drink. He states in his 'Methodus Fungorum', 1753, that a species of *Mucor* or *Byssus* can reproduce its kind ten times within a year, the commonest species of the latter (*Botrytis cinerea*) twenty-five times.

A. J. A. Battarra in his 'Fungorum agri Ariminensis Historia', 1755, was chiefly concerned with the systematic account of the species he found which he illustrated with

* This was a reply to an attack by J. G. Siegesbeck on Linnaeus and his system in the *Epicrisis* appended to his *Botanosophiae verioris brevis Sciagraphia*, 1737. Gleditsch, who describes Linnaeus as 'Botanicorum Spes, Decus atque Corona', probably received some help from Linnaeus. B. D. Jackson says about J. Browallius's refutation of Siegesbeck, 'Much of it, and that the most important, was undoubtedly from the pen of Linnaeus. Similar in some respects was the condition under which J. G. Gleditsch published his *Consideratio*'. The only reference to cryptogams which I can find in the *Epicrisis* reads—'Sic ipse Claris. Autor ultimae classi, qua dorsiferas et Muscos comprehendit, *Cryptogamiam* quandam tribuit, eo quod a Creatore veluti exlusa videantur a Theoria staminum, quodque Natura harum neget coniunctionem secundum stamina: quum interim copiose per solas radices propagentur'.

In his *Brevis Sciagraphia*, however, he divides the vegetable kingdom into two kinds, complete and incomplete: the former is distinguished mainly by having flowers and seeds. 'Vegetabile contra incompletum est, quod partibus iisdem primariis, vel plane destituitur, vel saltem adhuc de illis inter Physicos et Botanicos controvertitur; uti e.g. sunt Fungi, Agarici, Merulii, Lycoperda, Tubera.'

excellent figures, unfortunately not coloured. He has, however, an introduction which is well reasoned and critical. He argues against the belief that fungi are either freaks of nature or tumours—'ubi Supremi Opificis manus non lateat'. Species are constant, though rather remarkably he holds that they are restricted in distribution, those of Italy being different from those of France, which like Germany, England, and the rest of Europe has its particular kinds, a belief which accounts for his describing so many new species. The second point is their constancy of form, a species which has a volva invariably has it, another species invariably has pores and so on. He calls the mycelium a 'root' having the same function as that of higher plants, acting as a hold-fast and absorbing nutriment from the soil or from trees. Fungi growing on trees are not truly continuous with them in structure, and different species occur on different parts of the tree and their occurrence is dependent upon whether it is alive or dead. Fungal 'roots' may be slimy, more usually they form a fine net-work, but they may be cord-like as in *Phallus* and other Gasteromycetes; he figures them for many species with only an occasional exaggeration. An attempt he made to repeat Mazzuoli's experiments with the fungus-stone ended in his obtaining only its own fruit-body, *Polyporus tuberaster*.

He tried in every way to germinate the peridioles of *Cyathus* and sowed frustules of the fungus in appropriate soils, and watered them with decoctions of the fungus, with no result. He also tried to grow from its spores a fungus which he found on decaying oak-leaves: his experiment was made in 1749. The weather was suitable and after a week or two he found that there were small fungi on the leaves; three days later, 'cum maxima animi indignatione', he found that these had been devoured by insects. But the small fungi, though all similar, had been entirely different from those providing the spores. Battarra recalls that seeds of flowering plants do not always produce offspring similar to their parents because of hybridization, and says that Plancus showed that *Tithymalus Cyparissias* C. B. P. and *Tithymalus Cyparissias foliis punctis croceis notatus*, recognized as distinct species by many authors, can arise from one and the same root—a fact which would have not surprised him if he had realized that the differences between the two are merely the results of infection by the rust *Uromyces*.

Battarra retained an open mind on the subject 'perfecto nihil certi'.

J. Monti, 1754, made over three hundred experiments with moulds on the same lines as those of Micheli, but held that the latter's results were inconclusive, as moulds developed on vegetable substances indiscriminately whether spores were

sown on them or not, and that substances became mouldy even after boiling. Monti's results 'led some people into the dangerous theory of spontaneous generation'. The Comte de Buffon and J. T. Needham became the chief upholders of this belief. Needham was apparently attracted to the idea first by being shown some infusions by John Hill in 1746. Needham maintained that a productive or vegetative force exists which is responsible for the production of organized beings. He enclosed vegetable and animal infusions in vessels which were placed in hot ashes; this was assumed to sterilize the media, but animalcules were later found in them, though none had been observed there previously. Grains macerated in hot water became covered with mould, and the mould transformed itself into animalcules, which were often similar in shape having a swollen head and fine body. These results, supported as they were with the authority of Buffon, made a considerable stir. Their death-blow was given by L. Spallanzani in a series of papers, 1765-1777. In his last work he remarked that 'it is universally received, that the origin of every plant must be from some part of another plant; and it was probably the inability to discover that part, or to recognize the seeds, that allowed the belief of spontaneous generation'. Spallanzani worked principally with what was obviously *Rhizopus stolonifer*. Examining the columella under the microscope he remarks that the heads 'are shaped like mushrooms, or, to speak more philosophically, they are real mushrooms', and by a little manipulation of his figures illustrates this clearly. In a series of experiments he showed that the origin and increase of mould is nearly in proportion to the heat of the atmosphere, and that much better growth occurs under a receiver because of the humid still atmosphere. He made experiments analogous to those of Micheli, but much more numerous, diversified and connected. Sowing moist bread and various fruits with spores he found that the production of mould was accelerated and intensified. He comments upon the large number of spores formed and that they 'may be disseminated in such abundance as to enter into the composition of all animal and vegetable substances... it is the readiest method of accounting for the extraordinary abundance and universal existence of mould... one of the most reasonable hypotheses in philosophy'. He tried to grow the spores on many different materials—glass, stones, metals, writing paper—and concluded that 'certain circumstances are requisite for the expansion of the seeds, and these are found only in particular substances'. He tried the effect of heat and discovered the clue to Monti's results as 'the minute seeds or dust of mould possess the peculiarity of resisting a degree of heat, which no other seeds can support without losing the power of germination'.

C. Bonnet in a letter to Spallanzani suggests a further point 'When the vegetation of these minute plants ceases, in vessels hermetically sealed and exposed to the action of heat, it is more than probable that the numbers, which appeared on vegetable substances that had boiled from half an hour to two hours, came from the ambient air. The seeds must be of such extreme minuteness that we cannot wonder if they penetrate wherever air has access'. Struck by the amazing diversity in this class of beings Bonnet questions whether they all belong to the vegetable kingdom, or whether some may not approach the mineral or at least form a sort of connexion between the two*.

Spallanzani's experiments on moulds were generally regarded as conclusive, but many mycologists, even though convinced that 'seeds' were present in fungi, still continued to believe that some fungi at least could reproduce themselves without them. This opinion was held by C. H. Persoon, 1818, and C. G. D. Nees von Esenbeck, 1820, working on *Mucors* declared that fungi can just as well be formed by spontaneous generation from the fundamental elements as reproduce themselves by their sporidia. C. G. Ehrenberg in 1818 would not deny spontaneous generation, but two years later said he had not met with a single fungus whose origin he could ascribe to its working. E. M. Fries, 1830, expressed doubts about those fungi which were not autonomous (e.g. Rusts) and C. W. von Naegeli, 1842, had no doubt whatever that fungal endophytes had an origin by heterogenesis.

A belief in the doctrine of spontaneous generation of animalcules in organic infusions continued to be widely held for almost a century, gradually becoming involved in problems of putrefaction and fermentation. These two subjects had received attention from writers throughout the centuries, and so early as 1697 G. E. Stahl, known for his phlogiston theory, had distinguished three kinds of fermentation, that of beer, wine, and bread, acetic fermentation, and putrefaction and decomposition.

It was not until 1836, however, that it was recognized that living cells were concerned in these processes. Persoon had described the genus *Mycoderma* in 1822, with four species and the following year J. B. H. J. Desmazières wrote at length on the genus and described five species, one of which *M. Cerevisiae*†

* 'I wish a society of botanists would engage in the study of these plants alone. What do I say, "mould" only would demand their whole attention. Nothing is better adapted to make us forcibly feel the narrow limits of our corporal and mental abilities than applying to researches on the most minute productions of nature. All the finest faculties seem to vanish at the root of a stalk of mould.'

† Desmazières wrote the specific epithet as given here.

he found in humid membranes growing on beer; it is now known to cause a disease of beer. A second species was *M. vini* * which is 'la fleur de vin' used in the making of sherry. Desmazières was interested mainly in the morphology and general physiology of these organisms not recognizing their fermentative power. In 1836 C. Cagniard-Latour described the yeast-cells of beer as globular organized bodies probably of vegetable nature which increased by budding. He attributed the production of carbon dioxide and alcohol from sugar to their vital action. T. Schwann, independently rediscovered the yeast-cell in 1837 and regarded it as a plant—'Zucherpilz', which Meyen converted into *Saccharomyces*, though he doubted whether it was animal or plant. Schwann noted the differences between beer and wine yeasts and connected their growth with the process of fermentation; he also discovered the ascospores (endospores). F. T. Kützing in the same year, also independently rediscovered the yeast-cell, and although he did not observe budding he described the nucleus. He was led astray in a manner not uncommon in later years, and believed that yeast-cells developed into *Sporotrichum* and *Mucor* when removed from the liquid. Yeasts played a conspicuous part in the controversies about pleomorphism.

J. J. Berzelius, the famous Swedish chemist, immediately opposed the theory of the organic nature of fermentation, regarding it as due to a catalytic force. The chemical theory was vigorously upheld for many years by J. von Liebig until demolished by L. Pasteur in 1859. Twenty years later E. C. Hansen began his long series of researches in the Carlsberg laboratory which did so much towards making yeasts the best known of all fungi.

As the fungus-stone inclined many naturalists to consider that fungi had some connexion with the mineral kingdom, so entomogenous fungi influenced the tendency to regard them as having animal affinities. Though *Cordyceps militaris* is a common and conspicuous fungus in Europe it was a Chinese species, *C. sinensis*, which first received attention.

In 1726 R. A. F. de Réaumur gave an account of the fungus which the Chinese called 'Hia tsao tom tchom', i.e. plant during summer and worm in winter. He had received three hundred specimens from a Jesuit priest with the information

* This is given as the equivalent of two of Persoon's species, *M. mesentericum* and *M. Lagenae*. He regarded Persoon's names as unsatisfactory, and adopted the method of distinguishing the species as parasites are by the name of the host as in Rusts, 'par les noms des liquides sur lesquels ils se développent.' Persoon doubted whether *Mycoderma* is a fungus. Desmazières decided that it belongs to the animal kingdom.

that they were to be obtained hardly anywhere except in the palace at Pekin, as they grew only in Tibet and Szechwan. The specimens were broken and this was regarded as accounting for the absence of leaves, flowers, and stem. Réaumur's idea was that the caterpillar attached itself to the ends of roots—what he interpreted as roots being the fruit-bodies of the fungus; this explanation was repeated by C. P. Thunberg in 1775.

J. Torrubia, a Franciscan friar, in his 'Aparato para la Historia Natural Española,' 1754, described and figured a West Indian species. The main part of his account is translated in G. Edwards, 'Gleanings of Natural History': "Being at a Gentleman's country-seat, two leagues from the city of the Havanna in New Spain, on the 10th of February, 1749, I found some dead Wasps in the fields, (however they were intire, the bodies, wings and all, and indeed were perfect skeletons). From the belly of every Wasp a plant germinated, which grows about five spans high: the natives call this plant Gia; and as it is full of sharp prickles, their vulgar notion is, that the said prickles owe their growth to the bellies of the Wasps". Torrubia says that he made many microscopical and other observations but these are not detailed. He prints, however, an elegant set of verses written by a priest of which Edwards unfortunately gives no translation, but he reproduces Torrubia's figures [Pl. 7, e] colouring the plant green. But Edwards disbelieved the story, and is of the opinion that the parasite is the fungus (*Cordyceps sobolifera*) figured in his preceding plate †.

The nature of this fungus was first explained by W. Watson in 1763. Specimens were received of the 'vegetable fly' by Dr. Huxham from army and naval officers who had obtained them at Dominica. One, Mr. Newman, had stated that the fly buries itself in the ground in May and begins to vegetate. 'By the latter end of July the tree is arrived at it's full growth, and resembles a coral branch; and is about three inches high, and bears several little pods, which dropping off become worms, and from thence flies, like the English caterpillar'. An account of this extraordinary production, similar to the above was given also by Captain Gascogne. Watson thought

* The title page of Part III is dated 1764, but the British Museum (Nat. Hist.) copy has the inscription "Presented to the Trustees of the British Museum for the use of the Publick By their Most Humble Servant the Author", and the date is added: 'May 13, 1763'.

† Torrubia's fungus was probably *Cordyceps sphecochila* which occurs on wasps. Concerning this fungus A. Halsay, 1824, says that R. Mandianna, in Guadeloupe, 'noticed the wasp still living with its incumbrance attached to it, though apparently in the last stage of existence, and seeming about to perish from the influence of its destructive parasite'; the inhabitants call it 'la guêpe végétale'.

the relation quite repugnant to the usual order of nature, and, hearing that J. Hill had had the examination of some of them, wrote desiring to be informed of the result of his enquiries. Hill had received a box of specimens from Lord Bute, and wrote: 'There is in Martinique a fungus of the *Clavaria* kind, different in species from those hitherto known. It produces soboles* from its sides. I called it therefore *Clavaria Sobolifera*. It grows on putrid animal bodies, as our fungus ex pede equino [*Onygena equina*] from the dead horses hoof. The Cicada is common in Martinique, and in it's nymphal state . . . it buries itself under dead leaves to wait it's change; and when the season is unfavourable, many perish. The seeds of the *Clavaria* find a proper bed on this dead insect, and grow'.

A specimen was presented to the Royal Society, and Watson, after careful examination, agreed with Hill's 'opinion of the manner of this phaenomenon's being produced'. It was confirmed six years later by A. D. Fougereux de Bondaroy † for *C. sobolifera* and *C. sinensis*.

Hill seems to have been the first to point out the true nature of these fungi, but as our first President said about him in another matter 'Sometimes as Linnaeus says, a blind hen meets with a grain of corn'. Hill was both versatile and prolific. In 1755 P. Ascanius, when on a visit to England, had written to Linnaeus about 'Dr. Hill, the too famous

* Occasionally the stem of *Cordyceps sobolifera* is provided with a few short arms, which may be crowded about the middle or arranged alternately 'forming a kind of abnormal offspring'. The processes, or soboles, are conidial. *Isaria Sinclairii*, which is usually considered to be the conidial stage of the fungus, is known in Mexico as 'Chicharra' or 'Animal Planta'. N. Colin, 1793 (in an address read 1789), speaks of a zoophyte in the Ohio country which alternately is vegetable and animal, on the authority of a respectable missionary who had seen it, 'but would not have his name mentioned, as the matter may appear incredible: it is 3 or 4 inches high, and after having crawled about the woods, is fixed in the ground, becoming a plant with a stem through its mouth etc. It is analogous to the vegetable fly of Dominica' as described by T. Attwood, 'Natural History of Dominica', 1791, who says that 'from its body springs up a small plant, resembling a young coffee tree, only that its leaves are smaller. The plant is often overlooked from the supposition people have of its being no other than a coffee plant, but on examining it properly the difference is easily distinguished, the head, body, and feet of the insect appearing at the foot as perfect as when alive'.

† He records among his principal facts:—

'Que des supercheries faites dans le pays, changent cette singularité, et mettant des grains dans la tige de la *Clavaria* ou autrement.' This improving on nature by Chinese natives recalls the more successful trick of one of A. Henry's Chinese collectors which misled D. Oliver into describing a new genus, *Actinotinus*. 'It is made up of the inflorescence of a *Viburnum* inserted artfully into the terminal bud of *Aesculus chinensis*.'

naturalist of England. . . . I do not think any mortal has ever written with more impudence or more ignorance. His only excuse is that he must write in order to exist'.

J. T. Needham was attracted by the possibilities of the 'vegetable fly' of the West Indies which at the time he wrote, 1769, was apparently an article of commerce and he was able to examine fairly large numbers of them in different collections at Paris. He saw the perithecia, figuring them all down the stalk, but no 'seeds'—no one has ever seen these with certainty in fungi—and discussed whether the eggs of the fungus were in the insect or whether the fungus nourished the insect eggs. He also queries why only one species of insect shows the fungus, and why it always grows from the head. He made no attempt to solve these problems; he believed that transition between the fungus and insect could occur and vice versa, and that sufficed—as Guettard says, he would probably have explained the Scythian Lamb in terms of creative force*.

A. E. Büchner meanwhile, 1767, had criticized Torrubia's story, comparing it with the transformation of Daphne into a Laurel and Narcissus into a flower; he supported Hill's explanation. O. F. Müller in 1770 published a letter in reply stating that a similar entomogenous fungus occurs in Europe, *Clavaria militaris crocea* [*Cordyceps militaris*] described by Vaillant in 1723, and which F. Holm, G. Koenig, and himself had found in Denmark. Vaillant had not noticed that the fungus is entomogenous, and though J. C. Buxbaum, 1733, had figured it on an insect he had paid no special attention to the fact. Müller is convinced that the fungus is parasitic on the chrysalis and that one cannot regard the two as a vegetable fly any more than man or cattle as vegetable animals because moss sometimes grows on their skulls. The fungus never occurs except on a chrysalis. He holds that the spores need the juice of the dead insect for development, but according to his friends—'ingeniosa amicorum sententia'—the larva, while still in the earth eats the seeds of the fungus and, this being contrary to its nourishment, the insect dies and the fungus grows.

J. F. Gmelin, 1774, though not crediting the details of Torrubia's description, suggested that the figure he gave showed that he was dealing with a different kind of fungus from those described by Watson and Müller. It grew on the mature insect, and its shape was more suggestive of a fruticulose lichen than a branched *Clavaria*. He held that the

* Spallanzani in commenting on the use Needham makes of this to bolster up his general thesis says: 'Ce qu'il rapporte des graines de Champignon qui sont d'abord des Animaux seroit également ridicule, si Mr. de Munchausen & Mr. Linnaeus ne l'avoient pas inféré dans leurs ouvrages'.

relation between the plant and animal kingdoms lay in the fact that in the breaking down of their substances each provided material for the nutriment of the other.

G. D. Gründler, the following year, described how in 1769 he had taken seventy specimens of a caterpillar (*Lasiocampus quercus*, the Oak Eggar) to study their development; he placed them in damp moss, and *Cordyceps* appeared on one which had died. He thought that the seeds of the fungus were in the moss and that the warmth and moisture caused them to grow; the fungus might even be artificially produced by placing dead caterpillars in moss and providing suitable conditions.

Müller, in 1775, made another contribution to the problem in a paper describing the propulsion of spores in some species of *Clavaria* and *Lycoperdon* [*Spathularia flavida*], but this time added to the confusion. He believed that the giving off of a kind of smoke in successive waves is not produced by the movement of air, or by touch, or by elastic movement of the fruit-body, but by hazard. He says it is very easy to determine that the club is carpeted by cells filled with small thread-like bodies*, which are present in enormous numbers; they are white, similar to small fibres, and come out of the cells moving left to right: they are described as about ten times longer than wide and are obviously the elongated spores. When they are shed they simulate a mite's threads, later becoming like a spider's web.

The spores of the other species varied in appearance, and he asks what is the significance of these atoms, these delicate threads, these shining corpuscles. Are they powder, seeds, or a collection of small plants? The microscope teaches us nothing very perfectly. Are they worms or animalcules of an unknown kind? We here are hovering around Müller's well-known Monad theory. In his 'Zoologiae Danicae Prodromus' the following year he placed *Clavaria* with *Pennatula*, *Alcyonium* and *Spongia* in the section *Fungosa* of his group *Cellulana* of *Vermes*, with the character 'Osculis atomferis'. He included six species, the first of which was *C. militaris*. His hesitation about including other genera he explains in a footnote: '*Elvelae & Phalii* species, *Sphaerirae & Trichiae* mucidarumque pleraeque huc forte referendae, motum vero atomorum vere spontaneum in iis nondum vidi'.

J. L. A. Reynier (Regnier), in 1787, entered the controversy from the standpoint that organisms can reproduce from seeds without the intervention of sex, and that they can form by the

* The original says 'unzählbare, kleine, weise faserförmige Körperchen'. In what is presumably a translation of Müller's paper, though there is nothing to indicate that this is so, published in 'Observations sur la Physique', xiv. (1779), this is rendered as 'une infinité de petits animaux tout blancs'.

simple aggregation of organized matter—an unequivocal belief in spontaneous generation. Species of *Cordyceps* develop only on the residue of insects, and their shape is a consequence of the substances they derive. He interprets the appearance of two specimens he examined as showing that the *Cordyceps* had pierced the envelope of hairs and the chrysalis and broke forth from the body of the caterpillar; the two envelopes were torn by the fungus as it developed. If the fungus was merely attached one might think that its germ had been carried by the wind or deposited by some animal. This is untenable, however, for the seed must have penetrated the envelope and the chrysalis and have existed unharmed in the body before metamorphosis; it would be impossible for the seed to force its way through the strong continuous envelope; and, whether or not, seeds of fungi are unknown. *Cordyceps* thus draws its origin from the body of the insect itself when this is dead and has begun to undergo putrid fermentation. Animal substances differ from vegetable substances only by an excess of heat, and the passage of one to the other occurs in the stage of fermentation. The molecules have a tendency to unite and take on a form impressed upon them by the organism. In this way not only fungi but all cryptogams arise. Reynier tried to grow the 'bulbes' covering the head of *Cordyceps*, but without success; he examined the interior with a lens but seeing nothing admits that this may have been due to malobservation.

A. L. Millin de Grandmaison immediately pointed out that in Reynier's specimens the insects were already dead and partly disorganized, and so the tissue of the envelope was not so tenacious as to prevent penetration by an actively growing fungus. Moreover, the fungus might have penetrated the stigmata through which respiration takes place and so killed the insect by suffocation. He showed how Reynier had blundered about the reproduction of cryptogams and suggested that the fungus germ might have been absorbed with the food of the caterpillar.

Time and again all seems to be getting into something like order, and time and again there is a throw back to medieval mysticism. P. A. Engramelle, the entomologist, appears to have found nothing beyond belief. He accepted Torrubia's story and also that of le Bossu, who, in an account of his voyage to the West Indies, described a white worm which lived in old trees and changed into a small bush which had stems and leaves and reached a foot high; Engramelle's only comment was that perhaps there are an infinity of other worms with more extraordinary metamorphoses. Engramelle himself described in 1779 a 'Phalène radicante'. This moth had partly putrefied, having lost its legs and antennae, with

part of the wings destroyed, but the body little altered. From the edges of all the articulations of the body white, distinct, fairly thick threads arose about an inch long; they occurred also on the principal veins of the wings. These filaments were the supposed roots. L. C. M. Richard in 1780 pointed out how little like roots these were, and the absurdity of suggesting that they might take root and produce plants. His examination of the specimen showed that the filaments were fungal, and he described the fungus as a species of *Byssus*. He made the note the occasion for criticizing the hypothesis of the transmutation of animals into plants. His opinion was that the life and organization of the two kingdoms are totally different. Animal substances when decomposing may provide nutriment to certain simple plants such as moulds, and when completely broken down contribute to the development of more perfect plants: these plants, however, have a life entirely independent of animal substances—in themselves decomposing their constituent parts tend to approach earthy substances.

In 1781 T. Holm (later Holmskjöld) gave a clear account of *Cordyceps militaris* and its relation to its host, and also *Ramaria (Isaria) farinosa*, which may be the conidial stage, though this has not been proved. The full account was not published for several years*. Holm found *C. militaris* in 1762 and enthusiastically undertook to ascertain its origin and life-history: it is probable that he was the first to recognize that the fungus is entomogenous.

He found the fungus not only on the larvae of *Bombyx rubi*, before they change into pupae, which is its most common host, but on the pupae themselves of many caterpillars of various genera. He never found the fungus growing except directly from insects, and as he thought that spores were unable to penetrate from without he was of the opinion that the fungus gained an entrance otherwise: 'The origin of fungi, their growth and the whole of their structure display so great a skill, that we recognize in them the power of the supreme Artificer, who produced them and so providently and carefully preserves them that he has built the propagation of certain species on the ruin of some insects, who repay, as it seems, with their life for the eating of fungus flesh which they too greedily devour, a fact which is proved to us most clearly by the histories of

* The full text in Latin and Danish appeared with beautiful figures in *Beata ruris otia Fungis Danicis impensa*. The first of these splendid folio volumes was published in 1790, the second in 1799 (posthumously). The work caused a sensation because of its elaborate make up and its valuable observations. Retzius said it was 'the most brilliant work which had appeared up to that time'. It is not yet out of print: except for a few plates the material is still in the hands of the publisher.

Clavaria militaris and *Ramaria farinosa*'. The fungus develops gradually in the intestine and apparently poisons the insect. He included bits of the fungus in a puppy's diet, and it eventually vomited, but large dogs, and hens, eat twice the amount with no ill effect. *C. militaris* has a sharp taste like *Lactarius piperatus*, but *R. farinosa* is pleasant to the taste, though leaving a certain acridity.

Except that it is probable that larvae are more likely to eat spores than pieces of the flesh itself, and that a germinating spore is able to penetrate the skin, Holm's account leaves little to be added. Ehrhart had previously shown, 1788, that the fungus was not a *Clavaria*, but a *Sphaeria*; and Link, 1833, split off the genus *Cordiceps* (*Torrubia* Lév. ex Tul. 1853). Later mycologists adopted Holm's views, except F. W. Wallroth, 1842, who believed that the fungi which he called entomophytes (principally *Cordiceps*, which he named *Kentrosporium*, and *Isaria*) are of a special kind. They are produced in specially favourable conditions in the body of insects without the intervention of spores; *C. militaris* is too rare and too isolated to be produced in any other manner. Instead there is a persistent germ of the fungus in the body of the insect which begins its development with the start of decomposition, if both internal and external conditions are suitable. But Wallroth believed that the doctrine of spontaneous generation was proved for both fungi and algae.

A. de Bary in 1869 saw the germ-tubes of *Isaria farinosa* enter the stigmata of caterpillars on which they had developed from the germinating spores. His full account of the infection of caterpillars by *Clavaria militaris* is given in his classic 'Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien', 1884 (English Translation, 1887.) Germination of the ascospore takes place on the skin of the caterpillar if it is only slightly moist. The germ-tubes penetrate at once, and at any part of the chitinous skin. Here they enlarge into somewhat stouter hyphae, which branch and pass into the deeper layers of the skin, finally reach the inner surface, and pass between the muscles and fatty lobes. Then conidia are formed which at once enter the blood and are spread throughout the body, filling it by degrees with a dense mass. The blood diminishes in quantity, the insect loses its turgidity, and dies. Then the sprouting conidia develop rapidly and in one or two days the interior consists almost entirely of a dense web of fungal hyphae. This sclerotium-like mass can give rise immediately to fruit-bodies from any part of the surface. Thus fact is as fascinating as fiction.

Another aspect of spontaneous generation, that which may be called the view of Nicander, that fungi are Ζύμωσις κακόν χθονός.

continued to receive strong support. F. C. Medicus in 1787 put forward the theory that they arise from plants in their first stages of decomposition. An elastic and attractive force recombines the substances and juices separated in decay, together with a certain quantity of water and heat, and fungi result. This process he calls vegetable crystallization. The "seeds" of fungi are nothing but extremely fine portions of fungus matter which have not attained perfection. Reynier, who translated Medicus's paper into French, says that the theory of the origin of organic matter by vegetable crystallization is due to J. C. De Lamétherie, who, in his '*Vues physiologiques sur l'Organisation animale et végétale*', 1780, asks whether one cannot suspect agarics of having an origin approaching crystallization. For the most part they arise only on wood beginning to rot—are they not therefore also sometimes raised vapours of the wood which thus crystallizes, for nothing in the structure of an agaric is like that of plants? De Lamétherie, however, in his preliminary discussion to the volume of '*Observations sur la Physique*', which contains the translation, says that Medicus hardly proves his point, and in any event was treating again the question of spontaneous generation; it is necessary to recognize that the first production of organized beings was the result of some movement impressed on a portion of matter whether one called this Crystallization or by some other name.

Almost simultaneously G. F. Märklin, the younger, considered whether fungi were plants, or animals, or dwellings formed by insects. He states that most authors believed that fungi belong to the animal kingdom, and he asks why fungi grow only on bodies in course of decay if they have their origin from animals, and why only on soil and not on sand and stone. He ridicules the idea that insects can build up fungus bodies, and regards entomogenous fungi as parasites. Fungi are the second or last vegetation of plant juices. The slimy ingredients connecting the parts of plants are dissociated by fermentation, and these grow out into fungi of so many kinds and forms. Fungi are nothing but '*ein blosser Naturspiel*', but he ventures to hope that they will be retained in the plant kingdom.

A. M. F. J. Palisot de Beauvois criticised Medicus from the point of view of fungal structure, and was ridiculed by Reynier and answered politely by Medicus; physiology rather than structure was regarded as the deciding factor. There was also a slight controversy between Medicus and Märklin. These views continued for many years. Medicus stuck to his guns, and so late as 1820 he repeated them in Sprengel's '*Entdeckungen*', though a little modernity was added by introducing Priestley's green matter, and terms such as deoxydation and

hydrogenization, and he extended his range to include algae, lichens, *Chara pulchella* and *Orobanche ramosum* in addition to fungi, as generating spontaneously. Sprengel himself upheld the view that fungi arise from organic slime, in spite of what had been said about their origin from seeds. Such views stated with conviction were strongly supported and equally vigorously contested.

It seems remarkable that the schools of thought were so directly opposed. On the one side there was the belief that fungi are plants (or at least organisms) arising from seeds or spores, on the other the belief that in some way or other they arise from decaying organic matter, even by heterogenesis. For the most part there was no attempt at compromise. Indeed, so far as I know, only M. B. Borkhausen*, in his 'Botanisches Wörterbuch', 1797, tried to weld the two views. After giving summaries of the ideas of various writers, ending with those of the Micheli school, he asks 'Cannot this theory be united with that of Necker, Medicus and Märklin? Might not one think that in the fungus which has originated through a vegetable crystallization from the separate parts of the plants, small bodies might originate through a continued capacity for crystallization, and these small bodies, if they alight on a substratum prepared for them, might attract the dissolved parts of plants in the form of fungus-substance, and then by means of this and by the tendency to growth inherent in themselves might develop with a form similar to that of the mother fungus. Perhaps also these small bodies possess the power to infect and injure the plant juices through the fine openings with which plants are always provided, and through which they perspire and suck in; and, by hastening their disintegration, to prepare for themselves a suitable substratum'†. The attempt seems to have been still-born, though it was sufficiently ingenious to have led many astray if it had been widely known.

The Münchhausen doctrine with its various modifications gradually faded out of sight, but continued into the nineteenth century. Thus G. R. Treviranus, in his 'Biologie', 1803, saw no possibility of believing that all fungi arise from seed. If fungus powder is placed in moderately warm water it swells gradually and changes into oval, mobile animal-like bodies. If these animals are carefully watched they are seen to form

* Borkhausen had previously, in his *Tentamen dispositionis Plantarum Germaniae seminiferarum*, 1792, treated ferns and bryophytes, but left out fungi and the remaining cryptogams, partly because they have no true seeds and partly because he believed their classification would undergo considerable change owing to the researches of Hofmann, Tode, Hedwig, Batsch, and others. The statement remained unchanged in the second edition, 1809.

† Repeated, unchanged, in the second edition by F. G. Dietrich, 1816.

clumps from which threads arise and later moulds and toadstools. He had previously, 1802, placed all cryptogams in the zoophytes (Phytozoa). Similarly, the same year, A. A. H. Lichtenstein put forward the 'new theory' of the wonderful metamorphosis of terrestrial zoophytes into different fungus-genera. He believed that most cryptogams have the same origin. Like others he was doubtless confused by the Mycetozones, but his plate shows a fantastic series of stages from the mobile *Molecula organica* to a *Boletus*; apparently different genera are formed if development stops at intermediate stages.

J. Girod-Chantrons, in his 'Recherches chimiques et microscopiques', 1802, may be regarded as a supporter of this view in his experiments which dealt with *Conferva*, *Byssus*, *Tremella*, etc. In *Tremella* [*Gymnosporangium*] *juniperina*, and other Rusts, in Smuts, powdery Mildews and other microscopic organisms, he describes how animalcules, true polyps, arise when they are subjected to certain preliminary treatment. He declared that he had proved that such microscopic organisms were frequently, if not always, the result of the action of his new group of polyps, and argues, for example, that in the Rust of beans (*Uromyces Fabae*) the animalcules occur in the vessels of the host and are carried to the exterior by the circulation of the lymph. It is obvious that the drastic preparation of his material would kill any but the strongest organisms. 'Le vinaigre ne paroît pas leur nuire, non plus que l'acide nitrique, qui semble, au contraire, les raviver'. What he saw was doubtless some form of mechanical movement of particles, not Brownian movement because of their size.

With Lichenstein and Girod-Chantrons we seem to have reached the limits of absurdity. The most amazing aspect of the views of the supporters of the animal nature of fungi is that it seemed of no consequence what arose in water when spores or tissue were placed in it—protozoa, no matter what genus, larvae, no matter what group of insect—so long as something moved it was sufficient to demolish fungi as entities. The ready acceptance of the views of Münchhausen and Linnaeus was due to the fact that as little was known about infusoria anything could be believed.

C. L. Willdenow, in 1792, in commenting on the various ideas about the origin of fungi, says that the vegetable cristallization theory had the most followers, some going so far as to believe themselves capable of foretelling what fungus would arise from any leaf. He asks how it is possible to suppose any kind of crystallization capable of giving rise to a species so constant in its development as *Agaricus mappus*, and gives particulars of the habitats of such species as *Phallus impudicus* and *Psalliota campestris*; he says that he knows fifty fungi

occurring in pine-woods, in itself a sufficient answer to those who theorized in opposition to facts. 'Es ist so süß etwas zu träumen was noch keiner geträumt hat' *.

It is interesting to find that the first paper by C. H. Persoon, 1793, one of the outstanding mycological systematists, was on the subject what fungi really are. He had no hesitation in deciding that fungi are truly plants. He left for future discussion the question whether they are organic or inorganic, but listed five principal characteristics of organisms all of which fungi possess—differentiation, development, irritability, secretion, reproduction. Under each of these headings he then discussed whether fungi show more characters of plants or of animals. His conclusion is 'Ein Schwamm ist eine Pflanze die sich bloß als nackte Fruchtficationstheile darstellt'.

Though, as we have seen, Medicus maintained his original position for over thirty years, there was little support for it after the end of the century in relation to the increasing amount of mycological literature.

F. P. Schrank, in his 'Reise nach den südlichen Gebirgen von Baiern', 1793, referring to the theories of Medicus and Märklin, says both are wrong. It is true that many fungi and other forms of life seem to arise out of putrescence: he himself had seen it in *Agaricus truncigena* [*Pholiota mutabilis*], but there was no true transition from one to the other. If fungi arise in this manner why don't they grow on plants other than trees. Moreover, if the slime of a tree gives rise to a fungus, one should see traces of this inside the tree, but on slitting through a 'Keulenpilz' on the branch of a spruce he found the substance of the fungus was distinct from the wood, and penetrated only as strands. Further, he comments on the fact that fairy rings, common in fields and forests, are each composed of one species only, no matter what their extent or what change in vegetation they encounter in their growth.

By this time a considerable number of species had been described, and, on the whole, those who described them either definitely stated that they were plants or took it for granted. Those, however, who treated general questions still occasionally found it more easy to explain away fungi than to explain them.

J. F. Frenzel devotes the second part of his 'Physiologische Beobachtung', 1804, to fungi. His observations had extended over ten years, and he upholds Medicus with a wealth of physiological details, writ large. He regards the growth of

* 'When Willdenow flourished at Berlin, the opinions of naturalists on the nature of Fungi, their origin and reproduction, were so discordant that whoever wrote about them thought it his duty, either necessarily or legitimately, to form a new theory in order to win the favour of his readers'—L. R. & C. Tulasne, Preface to *Selecta Fungorum Carpologia*.

Polyporus tuberaster from the fungus-stone as a proof that fungi do not arise from seeds. The stone is known to contain roots and other parts of plants. The mixed lymph of this undergoes crystallization, and the mass so formed vegetates on the surface of the stone as fungi. Thus, the quickness of their development is explained, but the fact that they are always the same species not even commented on.

C. C. Haberle, 1806, was a supporter of Medicus, but his account of the development of *Sphaeria lagenaria*, which he found growing on the gills of agarics * and of *Merulius destruens* (= *lacrymans*) is of much higher quality than most of those adopting the theory. He states that many fungal genera have no existence, and the species in a genus are not sharply defined. He noted many modifications of the gills of *Lactarius*. Some specimens showed thickened gills which exuded milk and caused them to stick together. This milk acted upon by the air gave rise to threads which eventually developed into the *Sphaeria*. He reported his results to Ackermann, who considered that it showed the origin of life by crystallization and gave an account of his own observations on the mycetozone, *Lycogala epidendrum*, which arose from the sap of trees. Köhler, to whom he had also written, said that it was especially the bast which gave rise to fungi, and that the drops mentioned by Ackermann were the combination 'metamorphosé par le contact et l'influence de l'air en champignons'.

Merulius with its many forms lent itself readily to wishful thinking. How is it that so many fungi have a *Byssus*-like beginning? (i.e. a mycelium). It is because it rises from decayed wood by the action of warmth, moisture, and a still atmosphere.

K. A. Rudolphi, 'Anatomie der Pflanzen', 1807, states that he has often thoroughly examined the structure of Agarics, Boleti, Pezizae, Helvellae, and Hydna, and found that it was truly animal-like. He adopts the ideas of Medicus, and says there is no doubt that fungi are not plants, and calls them 'Afterorganismen'. How is it possible for seeds of *Corymbus* to be so abundant that they alight on a dead caterpillar and mould can be produced at will on all damp organic matter left for a short time in a room?!

But the tide was running out. F. E. L. Fischer, however, in his 'Beitrag zur Botanischen Systematik', 1812, regarded Rudolphi's standpoint as the correct one, and contrived to add a little originality: fungi arise daily out of organic chaos, and their small, ephemeral genera will provide work for mycologists for a long time. Though there is a good deal to be said this must be left for a special treatise. Reproduction

* The fungus was probably a species of *Hypocrea*.

is probably a delicate vegetable crystallizing around a germ, which cannot yet be called a seed.

J. F. Ackermann, in his 'Ueber die Natur des Gewächses', 1812, repeats the essentials of Medicus's views, basing his statements on what he had observed in *Boletus*, *Peziza*, *Lycoperdon* and *Clathrus* (by which he meant mycetozoa such as *Arcyria* and *Stemonites*). He regards parasites such as *Aecidium* and *Sphaeria* as showing a transition from higher to lower plant forms. Spore powder is the first principle of all vegetation. It gives rise to *Byssus* which transforms itself into fungi; if it meets with unfavourable conditions it is converted to minerals and gases—'das Pflanzenleben erstirbt, und nur das planetarische besteht.'

It is difficult to rid oneself of the impression that although many of the foremost scientists of their period interested themselves in fungi, most of them merely added to the confusion, made worse by the fact that no matter how unlikely their suggestions they were readily taken up in the attempt to understand this anomalous group of organisms. The difficulty of finding a place for them in the plant kingdom and relating them up to other groups still exists. Fungi were frequently regarded as a heterogeneous mass of indefinite organisms, the larger ones not very common, the microscopic ones widespread but few in kind. Even to-day 'many botanists, looking at Fungi from a distance, deem them a small province of the vegetable kingdom, although it is really the greatest, being analogous to that of insects among animals'*. 'Fungi probably exceed in number all other plants taken together' is an understatement, for Fries† was afraid that mycology would collapse under its own weight if all species were described. This failure to realize the enormous numbers of fungus species, their wide range of structural characters, and the physiological and phylogenetic importance of chlorophyll were responsible for much of the confusion of interpretation. If organisms must be either plants or animals then fungi are plants with a nutrition resembling that of animals as they do not possess chlorophyll. If, however, chlorophyll is the hall-mark of plant phylogeny the fact has to be faced that fungi probably never possessed it: the common assumption that they arose from different groups of algae is untenable by reason of structure, physiology, taxonomy, and probability; thus, for example, a parasitic red alga is a red alga and not a fungus. Fungi may be polyphyletic in the usual acceptance of the term, but as a group they appear never to have been related to algae, their only possible relatives, for algae became algae consequent on their

* E. M. Fries, *Syst. Orb. Veg.* p. 47 (1825). ..

† E. M. Fries, *Summa Veg. Scand.* p. 267 (1846).

becoming holophytic. They probably originated in colourless flagellates related to those in which algae presumably had their beginning, but we do not know sufficient about the Chytriales, or about the flagellates, to make reasonable guesses as to the lines along which development may have occurred, the number of these lines, or where they started. A consideration of the probable origin and relation of the different groups of fungi would take us away from the subject of this address, but it may not be out of place to add that I am convinced that the best approach to the study of mycology is by way of general botany, or, to put it more plainly, mycology should remain a branch of botanical study. But their vast numbers make it ridiculous that they should be 'plunged in unfortunate darkness beyond the other members of the vegetable kingdom' *.

Many of the ideas about the nature and development of fungi were dependent upon the belief in the presence or absence of seeds; and, if fungal seeds exist what are the organs of sex. It will be convenient to return to Micheli and outline the development of ideas about the structure of the larger fungi. It is unnecessary to stress the point that these had their part in the discussions that we have already considered, but as a rule this was not so prominent as might have been thought.

Few attempts were made to follow up Micheli's investigations either on the growing of spores or on the sex of agarics. The former have been mentioned. Gleditsch, 1747, examined the gills of different agarics and observed the three structures noted by Micheli, the 'male flowers' on the gill edge which he interpreted as stamens, the cystidia which he considered played a part in helping to separate the gills, comparing them with the stigmatic hairs of *Lilium*, and the seeds. As the stamens were so far from the seeds he supposed that the female organs must be hidden in the substance of the gill with small openings to receive the infinitely subtle molecules of the seminal powder, or at least genital vapour. He regarded fungi as monoecious with male and female in separate flowers. He found cystidia in many different fungi and not restricted to coprophilous species. The spaces between the gills are filled with seminal powder, later by the seeds themselves, arranged sometimes in fours, sometimes without order.

J. C. Schaeffer, in his 'Vorläufige Beobachtungen' in 1759, states that he was unable to find the apetalous flowers described by Micheli, and consequently denied that fungi had sex. He saw the cystidia, and the spores which he describes

* H. I. Tode, 'Fungi Mecklenburgenses selecti', 1790.

as borne singly on pedicels: the spores when they fall sometimes dehisce and pour forth a liquid. Schaeffer described the different shapes and colours of the spores of Basidiomycetes and the method of dropping them on white or coloured paper seems to have originated with him; he also used glass. He hung up a sporophore in a small room and found that the spores were distributed everywhere. The spores he thought best to regard indiscriminately as gemmae or a kind of bulbil: fungi enjoy a mode of propagation peculiar to themselves, and even the most minute fungus is the legitimate offspring of a parent like itself.

C. C. Schmidel, 'Icones Plantarum', 1762, figures *Coprinus comatus*, and says that on the margin of the gills he saw very slender transparent projecting, oblong or roundish globules which must be the male organs described by Micheli but the seeds he described as 'utrumque parietem dense vestiunt'.

J. G. Koelreuter followed up his classical work on the sex of the higher plants (1761-6) with 'Das entdeckte Geheimniss der Cryptogamie' in 1777. This did not do much to advance our knowledge of fungi, though it seems to have annoyed Necker who abominated all Koelreuter's ideas. His account deals with *Lycoperdon* [*Geaster*] *stellatum*. He considered the outer skin to be the male element which fertilizes the inner mass of seeds, maintaining that seeds cannot be produced without a male element. He regards fungi as plants, says that the presence of maggots is no sign of their animal origin, and points out that infusion animalecules occur when any vegetable substance decomposes. All fungi (like other cryptogams) have sexuality, all fungus-flowers and fruit rudiments are hermaphrodite, spores are true seeds, not dust, and fungi are propagated by this means more than by any other.

O. F. Müller in his 'Pile-Larven med dobbelt Hale', 1772, somewhat surprisingly deals fully with his Monad theory, which leads him to describe the occurrence of his molecules in the tubes of Boleti where, on the underside he saw stellate-bodies, presumably their habitations. 'These Monads and others likewise give to my mind a possibility whereby all organized creatures receive life and movement, are propagated and developed according to the modifications which the Creator has prescribed in his foundation; they mix themselves with the earthly parts of the nutritive substance, and in proportion to a lesser or greater admixture form floating or solid masses. They are imperishable, being like the Creator's foundation, so that nothing of that which is perceived by the human senses can destroy a single one of them. They lose life, and regain it once more. They collect into a lifeless mass, and remain so an indefinite time, indeed hundreds of years, until they

separate from each other, and again acquire life and freedom.' This theory has been regarded as containing the germ of many later ones in postulating imperishable minute particles: it did not help, however, towards reaching a proper conception of the nature and structure of fungi. Müller searched for the male flowers figured by Micheli both in Boleti and agarics, but without success, though he studied *Lepiota procera* which Targioni Tozzetti had pointed out to him in Florence as the fungus investigated by Micheli. He also studied *Armillaria mucida*, but, though he saw threads amongst the gills, and what appears to have been mycelium in the deposit of spores and slime shed on the ground, he saw nothing resembling Micheli's male flowers. In his articles on fungi in 'Kleine Schriften', 1782*, there is one on *Boletus bovinus*. Here again he refers to Micheli's discoveries, saying one sees the flowers on the plates, but no one has been fortunate enough to see them in nature except Gleditsch. He himself had for seventeen years sought for them in hundreds of fleshy fungi, but found not the slightest sign of them—either we see nothing at all or too much. He believes the spore-powder to be the seeds, and mentions experiments he had made to show this, though about one he says that though fungi came up it might have been that some might have come up without his doing so.

Two years previously in 'Florae Danicae', tab. DCCCXXXIV, Müller had published a plate of *Coprinus comatus*. Figures are given of magnified portions of gills: one shows the spores arranged in fours around circular structures, while at the edge there are suggestions that these are borne on sterigmata; the other shows what is apparently another view of these circular bodies, though no spores are drawn. Unfortunately the plates were issued without explanatory text.

We might well have disregarded the addition by A. M. F. J. Palisot de Beauvois in the 'Encyclopedie Méthodique', 1785, but that some of his ideas were adopted by A. L. de Jussieu in his 'Genera Plantarum', 1789.

Though he described fungi as true plants, and had a clearer idea of the nature of the mycelium of the larger fungi than most of his contemporaries, and though he was convinced that fungi possessed seeds, he did not accept the common view that these were the powder on the gills of agarics. This he interpreted as a 'poussière étrangère' carried there by the wind, or eggs deposited by insects: the true seeds, or molecules analogous to seeds, are contained under the pellicle of the gill, a view doubtless suggested by what he describes in *Peziza*. Further, though he agreed with Micheli's interpretation of the male flowers, he was unable to find the same forms observed and

* The date is that of publication by J. A. E. Goeze. No indication is given of when it was written.

thought that nature had been somewhat aided in Micheli's account, to which one might add that in his own account of the fertilization process in *Hydnum* and *Geaster*, nature seems to have been disregarded. In the latter, and puff-balls generally, he interprets the powder as the male element, and the female he discovered in a kind of network situated in the periphery of the fungus separated from the male powder by a fairly thick membrane. Fertilization occurs as the male and female elements escape from the orifice at the summit of the fungus, a mechanism which is described as interesting and quite curious.

The name of P. Bulliard is well known to mycologists because of the series of illustrations of fungi in his 'Herbier de la France: Histoire des Champignons de la France', 1791. Bulliard was a strong advocate for the belief that fungi are productions of the vegetable kingdom and have their origin from seeds, and, moreover, that they are the product of the seed of an individual of the same species. He hoped to be able to demonstrate that the 'blanc de Champignons' (spawn), which was sold for growing mushrooms, is not a mould but grows from a seed. All those fungi having their seeds distributed on the surface of gills have in the neighbourhood of the seeds some small vessels in which the spermatic fluid is contained. At a certain moment these fertilizing vessels burst open and scatter their fluid over the seeds: they open only when the air is sufficiently dry. These small vessels, of which he describes the shapes and distribution, are, of course, the cystidia, and the interpretation that they are the male organs was adopted by many later mycologists. The spores occur singly on small peduncles in agarics except in some dark-spored forms like *Coprinus*; other fungi have sessile spores. He mistook the spores of *Thelephora* and several other genera for spermatic vessels, and he decided that in *Agaricus digitaliformis* [*Psathyrella disseminata*] the vessels were scattered over the surface of the pileus. Truffles, *Nidularia*, *Lycoperdon*, and some other fungi do not have these vessels, but their spores are fertilized by the liquid which surrounds them. The spores of truffles resemble the mature fungus; 'il en résulte qu'on ne peut pas les regarder comme des graines, mais comme de petites Truffes toutes formées'*. The truffle is thus a viviparous plant.

* This view recalls that of H. Baker, on the spores of *Lycoperdon*. 'The Globules . . . had each a little Stalk or Tail. These are, evidently, so many minute Puff-Balls, furnished with Stalks or Tails to penetrate easily into the Ground'. 'The microscope made easy', 1742.

P. J. F. Turpin, 1827, was of the same opinion as Bulliard. 'La nature toujours prévoyante, toujours prodigue dans ses moyens, pour arriver à produire cinq ou six Truffes, établit dans la mère qui précède celles-ci des milliards de globules, tous centre de reproduction, mais dont

We may now retrace our steps a little to consider the classical researches of J. Hedwig so far as they dealt with fungi. In his 'Fundamentum historiae naturalis Muscorum Frondosorum', 1782, saying that some, by no means of inferior reputation, outlaw fungi from the vegetable kingdom and attach them to Trembley's animalcules, he regretted that in doing so they had not paid attention to the ordinary laws of the growth of plants, their origin, increase, and death.

Hedwig was the successful candidate for the St. Petersburg prize for which Necker competed. His essay was published as 'Theoria generationis et fructificationis plantarum Cryptogamicarum Linnaei' in 1784. It was badly printed, with many errors, and a confusing mix up of the plate numbers. A second edition, 'retractata et aucta' was published in 1798 with the plates coloured (two additional ones) and the text greatly amplified. His statements about fungi in the original essay are restricted to *Agaricus* and *Boletus*. The cylindrical bodies regarded by Micheli as stamens are not considered to be such by Hedwig; they are not present in every species, and where they do occur they remain unchanged even at the time when the seeds begin to ripen, which is not consistent with their being stamens for these usually vanish long before the fruit approaches maturity.

Hedwig traced the development of several species from the earliest stages. He considered that in those forms with a ring on the stem, or an arachnoid veil (cortina), the male organs are on the surface of these: where there is no such structure these organs are situated on the upper part of the stem or on the volva if there be one. Cutting young stages of a species of *Pholiota* before the veil was torn in growth he found that the inner surface was coloured brown. Under the microscope this surface showed transparent threads and among them a number of small, light brown globules in chains. Hedwig concluded that these globules were the stamens, and that fertilization occurs while the cap is still closely adpressed to the stalk. The seed, which is contained in the gills, does not lie quite bare, but is enclosed in certain vessels which in some species are distinguishable from the ordinary structure of the gills and from the ripe seeds by their size. He questions

l'immense majorité, affamée par quelques privilégiés, est forcée d'avorter. A leur tour ces globules privilégiés, devenus des vésicules, donnent naissance aux petits globules blancs . . . dont un, deux, trois, *jamais plus de quatre*, deviennent, en grossissant et en prenant de la consistance, par le moyen de nouveaux globules qui se développent en eux, des corps capables de reproduire. Ce sont alors autant de *Truffinelles*, auxquelles il ne manque plus que de s'étendre et de se remplir de nouvelles Truffinelles pour être des Truffes parfaites.'

whether the small cylindrical bodies on the margin of the gills, or on their surface, may be regarded as female pollen-conductors or serve some other purpose.

Bulliard later pointed out the obvious fact that Hedwig's male organs were spores which had fallen from the gills. It was a strange lapse on Hedwig's part not to realize this, for in the second edition he mentions that the powder is so abundant on the ring of *Pholiota aurea* that the yellow colour comes off it on being touched. The other structures he describes on the gill are obviously various kinds of cystidia: he later calls them spermatocystidia. Thus Hedwig's ideas were very like those put forward by Koelreuter for *Geaster*.

J. S. Kerner, in his 'Giftige und essbare Schwämme', 1786, gives a similar account. He considers that fertilization occurs while the ring is still attached to the cap. The ring acts as a male organ, the female part is none other than the edge of the gills.

Hedwig's great contribution to mycology, however, was in his 'Descriptio et adumbratio Muscorum Frondosorum', 1787-97 (1789). There were two editions of this sumptuous work, one in Latin, the other in German, both dedicated to George III. In his St. Petersburg thesis Hedwig had figured asci containing spores in *Lichen [Physcia] ciliaris* 'quasi intra loculos evidentur conspiciuntur granula nigra in columnulam quasi conglomerata'—but now he described and figured asci in so clear a way that he established their existence once for all. He used the term theca for the structure enclosing the spores, a term he had previously coined for the sporangium of liverworts and mosses. Twenty Discomycetes were described and illustrated, and for them he proposed the genus *Octospora*. The essential part of his diagnosis reads: 'Thecae seminales membranulosae, elongatae, numerosissimae, ut plurimum stupa filamentosa cinctae; utrisque inter se non cohaerentibus, seminibus octo foetae.' He assumes the presence of sexual organs. The male organs are situated on the edge of the unopened disc and are either club-shaped or hair-like, and tear apart as it opens. Where he could not see them he thought it was because the fungus was too old or the structures too small. The female organs, which he sought on the concave side of the disc between the paraphyses, were less often found. Previous to Hedwig's discovery all cup-shaped fungi were usually classed together more often than not as *Peziza*, though Gleditsch had used this name only for *Cyathus* and *Crucibulum*. Hedwig, in establishing this separation on a sure foundation, retained *Peziza* in Gleditsch's sense and erected *Octospora* for cup-shaped species; presumably he regarded Gleditsch's genus *Elvela* as too extended for his purpose. On the other hand, by showing that some species of lichens also had thecae

with eight spores he proved the close relation of lichens and fungi.

In the second edition of this 'Theoria', 1798, he figures asci in a species of *Sphaeria*. He interprets the very young asci as male elements, the contained granules being pollen grains, and the larger asci as representing the female organ—a sporangium containing true seeds.

We have seen that Schaeffer regarded the spores of agarics not as true seeds but as gemmae or bulbils. G. R. Boehmer, in 'De Plantarum semine', 1785, agreed with Koelreuter that fungi possess seeds, but thought that these had a kind of minute power of fertility and, like bulbils, were produced in a state capable of germination without previous fecundation. Compared with the nobler seeds they seem imperfect and are usually so minute that few, however sharp-eyed, could ever discern whether they are naked or provided with an integument.

J. Gaertner in his classical 'De fructibus et seminibus plantarum', 1788*, adopts a similar view—fungus granules are gemmae or buds, not seeds. Fungi deserve the first place amongst asexual plants and 'it is clearer than the mid-day sun that these granules have nothing in common with a true seed except their external form'. His theoretical reasoning concerning their origin from cortex and medulla need not be considered, but he gets very close to recognizing essential differences when he states that the radicle, or germ-tube, which they produce on germination, is derived from their own integument and is continuous with it; it may indeed be broken, but is never cast off. This may be taken to mean that fungal spores do not contain an embryo, but I cannot trace that Gaertner said so definitely. L. C. Richard, in his 'Démonstrations Botaniques ou Analyse du Fruit'†, 1808, appears to have been the first to draw the distinction 'Les *Sporules* différent des Graines, non seulement par leur mode de formation, mais encore et surtout par leur défaut d'Embryon'—a distinction which was not disputed until the discovery of the 'seeds' of Pteridosperms a century later.

The term spore (*spora*) was coined by Hedwig in 1798; he does not appear to have had in mind any distinction between spores and seeds, except that the former arise in special

* This work was dedicated to Sir Joseph Banks who had supplied him with a collection of seeds.

† This was written by H. A. Duval, who attended Richard's lectures 'depuis plus de dix ans'. He was authorized to publish it by Richard. The copy in the Department of Botany, British Museum, is inscribed 'Exemplaire corrigé par l'Auteur : et donné à M. Robert Brown, comme un témoignage d'estime. Richard'.

conceptacles which he calls sporangia*. The term was applied to all groups of cryptogams, but throughout the work *semen* and *spora* are used indiscriminately as in describing *Agaricus*.

Other authors found the term exceedingly useful, though arguments long continued about the necessity for it and about the equivalence of spore and seed. Thus Willdenow in a preface to J. F. Rebentisch, 'Prodromus Florae Neomarchicae', 1804, protested that spore expresses nothing more than the old word seed, and feared that the introduction of special terminologies for cryptogams would lead to a disturbance such as formerly occurred at the construction of the tower of Babel; and J. E. Smith wrote in Rees's 'Cyclopædia', 1819, under the heading *Sporae*—'a name given by some botanists to the seeds of certain cryptogamic plants; by which they seem to imply a doubt of their being truly *semina*, or exactly analogous to the seeds of plants in general. We know not on what such doubts are founded. If the parts in question be produced or perfected by sexual impregnation, they are to all intents and purposes real seeds, nor does any peculiarity, or apparent simplicity in their structure, invalidate the propriety of their being so called. . . . If such apparent seeds be not the offspring of sexual impregnation, they are *Gemmae*'. Even such eminent mycologists as L. & C. R. Tulasne, and so late as 1861, objected to the statement that spores differed from seeds in not containing embryos: the whole spore can be regarded as an embryo, made up of one or more cells, presenting a faithful picture of its purely parenchymatous parent. In whatever way they arise they are seeds of their own kind—indeed, true seeds in a Linnaean sense.

Hedwig's clear drawings (Pl. 6, *d*) were the first which showed a proper analysis of the microscopical structure of fungi, and they had a great influence on the development of mycology. Once it was clearly shown that spores are formed in a definite manner and in definite numbers there was decreasing opposition to the view that fungi can be accounted for in a normal manner of origin, growth, and development. Immediately there was abundant confirmation of the easily ascertained fact that in certain fungi eight spores are enclosed in club-shaped sacs. But there was more than confirmation, for asci were described in some fungi where they do not exist.

In 1794 Persoon began the series of contributions to

* At quam primum inde exorta propriisque suis velamentis contenta proles, sistens ovulum vegetabile, vulgo semen dictum, saepius a me vero graeco vocabulo spora indigitatum, insuper alio receptaculo comprehenditur, uno aut pluribus; idem hoc sporangii nomen in genere sortiri.

systematic mycology, which may be regarded as the foundation of modern classification. His sixth order, Hymenothecium, comprised the Discomycetes and Hymenomycetes, and was defined as 'Receptaculo ut plurimum carnosio membranæ (Hymenio) ex thecis in seriem digestis constanti, toto adnexo.' The conception of a hymenium was new—a skin appearing continuous to the naked eye covering a layer composed of the spore-bearing organs. The assumption seems to be implied that these organs are asci, though it is nowhere stated that they necessarily enclose spores. Two years later he drew the spores in *Corticium caesium* and described them as clearly arranged in fours similar to what is found in some agarics.

H. F. Link in 1809 adopted the main outlines of Persoon's classification, but in his definition of his fourth group, to which he restricted the use of the name Fungi, he stated that sporidia are contained in series in elongated cells, the surface being the closely packed tips (thecae). He says that though naked spores have been attributed to *Agaricus*, *Boletus*, etc., none the less these forms are provided with thecae, and in his plates, drawn by Ditmar, the spores of agarics are so shown. The arrangement in fours known in *Coprinus* since 1729 is explained by stating that unlike agarics and all other 'Fungi' which have a single series of enclosed spores in the theca, *Coprinus* has four series, and drawings are given illustrating this. The drawings are copied by E. G. Nees von Esenbeck in his 'System der Pilze und Schwämme', 1817, to illustrate *Coprinus cinereus*; in all other agarics he shows one row of spores in the ascus, a term he introduced in place of the more generalized theca*, restricted to bryophytes. A. C. J. Corda's plate of *Agaricus (Coprinus) micaceus* [Pl. 6, f] shows the series of four in surface view but not in longitudinal view; his *Clavaria pistillaris* [Pl. 6, e] shows four spores inside asci.

All accepted Link's interpretation—Brongniart, Chevalier, Desmazières, Duby, Greville, Klotzsch, Krombholz—and this proceeded for a quarter of a century. Persoon, in 1819, added *Thelephora caryophillea* and *T. phyllacteres* to *Corticium caesium* as having spores in tetrads, but there was no recognition of the fact that the spores of Basidiomycetes are borne externally, although it is as simple to observe as that the spores of Ascomycetes are borne internally. Indeed, it was obviously difficult at times to make the observations fit in with preconceived ideas. Persoon stated that the spores in the ascus were often extremely small and sometimes imperceptible. C. Vittadini, in his 'Monographia Tuberacearum', 1831, gives the first figures of basidia, both unispored and tetraspored,

* Thecae, den ich, da der Ausdruck doch noch öfter für die Mossfrucht gebraucht wird, mit der entsprechenden Benennung: Asci, Schäuche verstauchen will, bezeichnet zu werden pflegt.

the former containing internal spores and the latter, in *Bovista* *, showing two stages indicating that internal spores pass to the exterior by a method similar to that still sometimes regarded as the hypothetical phylogenetic origin of the basidium †. But, in a remarkable way, attention became concentrated on the hymenium of Basidiomycetes, several investigators independently publishing their results.

B. Ascherson, in a short note which was repeated in several botanical journals in 1836, stated that he had made numerous microscopical researches on the 'higher fungi' and had come to the unexpected conclusion that instead of being contained in asci their spores stand on small stalks on cylindrical structures, usually four, but apparently three in *Boletus*. His research was carried out on several genera, and he believed that his results would be found to hold for the whole order 'Mycetes'.

J. H. Lévillé announced his results on the study of the hymenium to the Société Philomatique de Paris, in March 1837. He stated that the Hymenothecii of Fries's 'Systema Mycologicum' comprised genera which were not related and that the group should be divided according to the structure of the hymenium. In *Agaricus (Coprinus) micaceus* the gills, in profile, show two kinds of organs; projecting diaphanous conical or cylindrical vessels which he calls cystidia, and less prominent, closely packed structures ending in four points, each bearing a spore, which he calls basidia. Cystidia are absent from a large number of species, but basidia are always present. He contrasts this with what is found in fungi with asci and divides Fries's Hymenotheci into Hymenomycetes, or Basidiospori and Hymenothecii, or Thecospori. C. Montagne, at a meeting of the Society the following week, controverted Lévillé, and said he had found the spores contained in the utricles or asci which form the hymenium. From a note in a paper published the previous December it appears that Montagne had completed some research on the subject. The full account was referred to Mirbel, Turpin and Richard for report: the report was published in January 1837. It is stated that twenty-four agarics were studied, and in them the tip of the utricle is pushed forward to form the sterigmata and the spores rather than that the spores pass through minute pores to reach the exterior. Montagne, an outstanding cryptogamist, became convinced, however, of the truth of Lévillé's interpretation, and his full monograph was never published. Lévillé's paper was sent to A. Brongniart and

* Asci tetraspori . . . cum propius sporidiis emersis ac longo pedicello suffultis.

† Asci numerosissimi, oligosporei . . . Sporidia emergentia ascorum apici, pedicello vestientis, congesti. [*Hymenogaster*.]

A. Guillemin, and their report, written by Brongniart, is published as an appendix to Lévillé's full paper which came out later in the year. The paper is a model of its kind with four plates (Pl. 7, *d*), three by J. Decaisne, who gave so much help to the adjudicators that they appear to have co-opted him. Lévillé regards the spores as true seeds and gives an analysis of the hymenium, basidia (a term coined with Guillemin), cystidia, and the remaining structures in the hymenium which he calls paraphyses. He states that the veteran Persoon, to whom he demonstrated his results, could not conceive how organs so constant and so easy to see as basidia could have escaped the notice of the great number of mycologists who had made observations with the microscope; de Jussieu also recognized the constancy of basidia. Lévillé states that it took him seven years to make out the true nature of the basidium of *Tremella*, but in his twelve years' study he investigated agarics, Boleti, *Thelephora*, *Hydnum*, *Clavaria*, etc. Basidia are four-spored, bispored, or monospored.

Brongniart and Guillemin fully confirmed Lévillé's results which, in their opinion, were so new and so contradictory to the opinions of recent authors justly noted for the exactness of their researches, that they examined as many species as possible, and recorded that the basidiospores of *Cantharellus cibarius* are normally six or more, rarely five or seven.

Also in 1837 Corda figured basidia with four spores in *Coprinus petasiformis*. He described the basidia as free asci with four naked, pedicellate spores. He also described and figured cystidia and paraphyses.

The following year M. J. Berkeley, the father of British Mycology, published a paper on the 'fructification' of the pileate and clavate Hymenomycetes. Unaware of Lévillé's paper he produced one in every way as valuable. In the volume on fungi in 'English Flora', 1836, Berkeley had already said that in *Agaricus (Clitopilus) prunulus* the gills are 'covered with very minute conical papillae, ending in four spiculae. Sporules . . . often seated upon the spiculae' and had described the quaternate arrangement of spores in *A. (Psilocybe) cernuus*, *A. (Psathyra) bifrons*, *A. (Psathyrella) gracilis*, *A. (Psathyrella) disseminatus*, *A. (Coprinus) semiovatus*, etc. The note of Montagne stimulated him to make a more intensive study of the hymenium to which his attention had been directed for some time; it was only after the report of Mirbel, Turpin, and Richard, when he had almost completed his observations, that he found that his interpretation was different. 'The acquisition of a more powerful doublet than I before possessed determined me to examine accurately the structure in *Coprinus*, in Link's account of which I did not feel confidence'. Berkeley found four-spored sporophores (basidia) to be general in

Hymenomycetes, though occasionally two-spored (e.g. *Agaricus* (*Lactarius*) *flexuosus*), five or six-spored (e.g. *Cantharellus cibarius* and *C. tubaeformis*), one-spored (*Cantharellus fissilis*), three- to four-spored (*Hydnum repandum*). 'The essential character of hymenomycetous Fungi appears then to consist in a hymenium composed of closely packed sporophores, which support on spicules a generally determinate number of spores'. Cystidia are described as utricles, but receive no special treatment (Pl. 7, c).

A year later, 1839, Berkeley extended his observations to Gasteromycetes, where he was able to establish the fact that basidia are present in *Lycoperdon*, *Bovista*, and *Mutinus*; he suspected their occurrence in *Scleroderma*, where L. Tulasne found them in 1842.

A French translation of Berkeley's paper was published. The translation and communication was made by Montagne, who, apparently, was converted to the view which had been arrived at independently by so many observers. The list of these, however, is not complete. Yet another account of basidia appeared, that of F. Klotzsch in A. Dietrich's 'Flora regni Borussici', 1838, who gives plates of twenty-one Basidiomycetes in which basidia are figured accurately—*Agaricus*, *Boletus*, *Daedalea*, *Thelophora*, and *Hymenangium* [*Rhizopogon*]. He goes so far as to include 'sporae quaternae pedicillatae' in his definition of *Agaricus* and other genera. Cystidia are regarded as anthers, and paraphyses are also noted. The cystidia develop at the same time as the spores. Spores which have fallen from the basidia and are stuck to the basidia, when removed with a needle, will germinate, for they have been fertilized by the liquid which oozes through the wall of the cystidium; the cystidia, being closed, collapse when empty. The first-formed spores which fall to the ground are incapable of germination because they have not been fertilized; most of those formed later develop normally. The following two volumes of the flora published in 1839 and 1840 respectively contain nineteen plates of Basidiomycetes showing basidia and spores. Klotzsch clearly recognized the difference in structure between Tuberaceae and hypogaeal Gasteromycetes.

P. Phoebeus, in his 'Deutschlands kryptogamische Giftgewächse', 1838, has eight plates of Hymenomycetes and figures basidia, which he calls Träger, together with the spores forming a Tetrad. A full account of his researches appeared in 1842*, but a note states that it was communicated on March 6th, 1837†. This is the longest of the monographs on hymenial structure and is far more detailed than either of the others. It is regrettable that owing to the delay in publication it did

* Nov. Act. Acad. Not. Cur. xix. 171-278, 1842.

† Lévillé's paper was communicated March 18th, 1837.

not receive the attention it merited, for it has an excellent account of the occurrence and structure of cystidia, which he called paraphyses. The different genera are described separately, and one has the feeling that if this monograph had been the first to appear the value of cystidia as diagnostic characters would have been realized forty years before it was and, moreover, would have been more widely recognized. Among other points noted by Phoebus was the occurrence of different generations of basidia in *Coprinus micaceus*, and the large cystidia ('similar to colossal paraphyses') of *Coprinus comatus*, which he regarded as having the function of bridges.

The facts just related appear to be a remarkable illustration of the way knowledge advances. It is perhaps more usual for someone more discerning or more brilliant than his fellows to make some discovery. If his contemporaries are in a receptive state the controversies which arise consolidate the position and knowledge advances: if not, the matter remains either as a curiosity or is for the time forgotten. In the present instance one cannot pretend that the discovery required anything beyond exact observation: the facts are such that they can be, and indeed are, confirmed in a first year's practical botany course, though their recognition was not so simple to accomplish with doublets. But simultaneously—for apparently none knew of any other investigations until his own was complete—Ascherson, Berkeley, Corda, Klotzsch, Léveillé, and Phoebus startled their own coteries by what was an epoch-making discovery, as revolutionary in its effects on the understanding of the structure and classification of fungi as it was simple to confirm. It is of little consequence to assign priority in the discovery; a statement by Berkeley in 1842 puts the matter in its proper perspective. 'The eyes of modern mycologists were for years blinded by Link's celebrated paper, or the real structure would long since have been recognized. The modern re-discovery is due to Ascherson: at least he is the first who made it known.' It should be added, however, that Corda, in his 'Icones Fungorum', III, 1839, in giving a history of the discovery, states that, when he was in Berlin in 1833, he described the spores borne on basidia and exhibited to the Royal Prussian Academy of Science ten figures which he reproduces (together with thirty-one others), showing the structure of the hymenium and spores, but the greatest German microscopists would have none of it, the quaternary arrangement was false, the cystidia, and partly also the basidia, were insect eggs.

All except Ascherson drew and described asci containing internal spores in contrast to the basidia with external spores.

Nowadays it is a little difficult to understand the search for homologies in the pre-Darwinian period unless one bears in mind that the so-called natural system of classification was making rapid progress and the need for discovering some underlying scheme of nature, some unity of plan, brought homologies constantly to the fore. The general belief in the constancy of species prevented any reasonable explanation of the obvious relationships other than that expressed by Fries in 1815 that it is 'quoddam supernaturale'. In his 'Systema Mycologicum', 1821, 'le bréviaire de tous les mycologues' he rejects Bonnet's notion that there exists a simple series or chain of natural affinities and carefully distinguishes between relations of affinity and relations of analogy. ('Quo magis in superficie acquieverunt naturae scrutatores, eo magis analogae cum affinibus commutarunt') He arranges fungi in four circles (the largest divided into two), having in the circumference a point of perfection or typical group, the centrum, and radii which lead from one centrum to another. In our 'Transactions' for 1823, W. S. Macleay* compared Fries's system with the quincuncial system which he had himself proposed in 1819 for the classification of insects, and showed that they were fundamentally the same. The 'Systema' did for mycology what the 'Species Plantarum' did for flowering plants. It was followed by a series of works ending with the 'Hymenomycetes Europaei', 1874, which are the bed-rock of mycological taxonomy.

It is not without significance that the division into Ascomycetes and Basidiomycetes agrees fairly closely with the sections of the Class Hymenomycetes in Fries's 'Systema Mycologicum', 1823, where his first two orders Pileati and Clavati are almost entirely Basidiomycetes, and his Mitrati and Cupulati are Ascomycetes (Discomycetes)†: the Pyrenomycetes are placed in his second Class, Gasteromycetes.

The clear cut division between the two kinds of spore-formation were not, however, readily accepted. Fries, for example, in 1849, wrote, 'In my opinion all sporidia are reduced asci, and all genuine spores are produced in an ascus that is in general rapidly dissolved away'. Fries used the term sporidium as a synonym of spore, but also as a diminutive of spore, or even for a granule resembling a spore; conidium

* The son of Alexander Macleay, Librarian of the Linnean Society of London (1796-8) and Secretary (1798-1825). 'Analogical resemblances... Lamarck first called attention to this subject, and he has been ably followed by Macleay and others.' C. Darwin, *The Origin of Species*, 1859, p. 427.

† These four orders comprise the 'Evoluti. Ascis perfectis'. The remaining orders, Tremellinae and Sclerotiaceae are described as 'Prototypi. Ascis imperfectis, nullis'.

(gonidium, Wallroth) was coined for those granules 'separated from the flocci as bare and quite simple bodies'—there cannot be two kinds of sporidia on the same plant. The term sporidium had been introduced by Link in 1809: he used spore for those granules where it was not established whether they were seeds or not, sporangium for the enclosing structure where such was present, and sporidium when it was doubtful if he was dealing with a spore or a sporangium.

Berkeley in his 'Introduction to Cryptogamic Botany', 1857, distinguished between naked spores and sporidia enclosed in a distinct sac; his Sporiferi comprised Hyphomycetes, Coniomycetes, Gasteromycetes, and Hymenomycetes; his Sporiidiferi, Ascomycetes and Physomycetes.

M. J. Schleiden, 'Grundzüge der wissenschaftlichen Botanik', 1842, describes the basidiospore as possessing a double wall: 'the external membrane of the Fungus-spores cannot be compared with that of the Moss-spores, or the pollen granules . . . it represents a spore-case' *.

H. Schacht in his 'Die Pflanzenzelle', 1852, held that the distinctions drawn between the methods of formation of ascospore and basidiospore are of little value; the basidiospore is formed in the dilated apex of a sterigma as if it were in a true ascus growing with it and adhering to it †.

A similar view was put forward by H. Hoffmann, in 1856, who stated that both basidiospores and ascospores are produced in asci, sometimes singly (*Agaricus*, *Tuber nuciforme*), sometimes several together (*Peziza*, *Phragmidium*). In the first type the spore adheres to the mother cell and is dispersed closely wrapped in it; in the second the spores, when ripe, are shot away.

Even such an outstanding observer as de Bary was led into doubt by observations he made on *Armillaria mellea* where, on the gills, he found ovate asci which were afterwards shown to be those of *Endomyces decipiens*. He conjectured that

* Schleiden's opinion of mycological investigators was not high. 'Almost all the works that have hitherto appeared on the lower *Fungi* are wholly useless, and may, without farther consideration be cast aside, since the work must again be commenced from the beginning. Investigations are of no value where they do not trace the composition of the forms from the individual cells . . . I must confess that I find it quite impossible to determine one of the lower *Fungi* from the ordinary descriptions, as they do not express what nature exhibits. Even delineations are not often of much avail. This arises from the fact that in many cases the specific difference does not certainly rest in the plant, but in the observers, their instruments, and the magnifying power used.' His 'own limited observations', however, are trivial, and not always accurate. The statement was retained in the 1861 edition of the 'Grundzüge'.

† He also considered that the sporangium of *Mucor* was analogous to the ascus of truffles.

there was close relation between Basidiomycetes and Ascomycetes, Basidiomycetes being the conidial forms of perfect existing Ascomycetes. So late as 1884 he stated that the parasitic nature of the *Endomyces* had not been shown, and hinted that his observation that the ascus proceeded directly from the hyphae of the pileus might be correct.

C. H. Peck, 1872, described the spores of *Agaricus* (*Hebeloma*) *Ascophorus* as 'produced in fragile globose asci borne on a thick, tapering, penetrating peduncle . . . a dozen or more in each ascus'*. The record by F. L. Sautermeister in 1876 of ascocarps on old shrivelled fruit-bodies of *Exidia recisa* hardly seems worth mentioning, for although he expressly stated that they could not be parasitic they obviously were. Masee, 1889, says that though the statement of Sautermeister and others had not as yet been corroborated 'even should this be done, it could not be considered as anything very extraordinary'.

From the beginning of the study of mycology the question of sex was always in the minds of those interested in fungi, just as it was for other groups. Several of the suggestions made have been mentioned, but without attempting to trace their origin and development.

The first recognition of a sexual process was made by C. G. Ehrenberg, who, in 1818, described and figured conjugation in *Syzygites megalocarpus*, a species better known by the name of its conidial stage, *Sporodinia grandis*. He gives a careful description of the fungus, and goes into the question whether it is to be considered as an animal or a plant, an alga or a fungus, and regards the fusion as sexual, or at least analogous to sexual (Pl. 7, a). Nees von Esenbeck, 1816, had classed *Mucor* and other filamentous fungi as 'Fadenpilze, Luftalgen', and Ehrenberg took this suggestion into account. He decided that *Syzygites* is a fungus corresponding to the conjugate algae and places it in his Ascophorae (*Ascophora*=*Mucor*). The conjugation shows such a close resemblance to zygospore

* Berkeley (1875) examined a specimen of the fungus and interpreted 'the bodies in question as analogous to the hispid bodies which occur on the gills of some species of *Marasmius*', i.e. cystidia. J. de Seynes (1875) supposes that 'it is a mass of substance exuded from the extremity of the Cystidium, that must have been taken for an ascus borne on a penetrating peduncle', the illusion being due to spores caught up in the secretion. C. H. Kauffman (1926) refers to these 'unique bodies' as reminding one of 'certain metalloïd bodies in the hymenium of other basidiomycetes. They are sac-like with granular or blocked-out contents, projecting very slightly above the basidia except when fully developed, apparently with a rather narrow pedicel below . . . This uniformity of occurrence is not likely explainable on the supposition that a parasitic fungus is present in the gills of this species. I believe them to be a normal development belonging to the life history of the species.'

formation in *Spirogyra*, which had been known from the time of Gaertner (1788), that many were inclined to regard *Syzygites* as an alga. Thus L  veill  , so late as 1846, in placing it after *Mucor* and *Pilobolus* * does so with a query '*Syzygites*, an *Alga aerea* ?'

Pringsheim's researches on the Saprolegniaceae (1851) and de Bary's on the Peronosporaceae (1852) are mentioned later. De Bary next turned his attention to Ascomycetes. The first species he investigated was *Pyronema confluens*, a species which has been studied frequently since, and around which controversy still wages. Tulasne in 1860 had recognized large sessile grouped ascogonia, but did not understand their function. De Bary three years later showed that they are female organs and that they become fused by their broad terminal protuberance to antheridia formed on the fork of the same hyphae.

Following this there was a series of studies by de Bary, Tulasne, Woronin, Fuisting, and others which showed that ascogonia and antheridia are present in Erysiphaceae and *Eurotium*, and that ascogonia without antheridia occur in *Ascobolus* spp., *Peziza* spp. etc., while two unicellular filaments fuse in *Eremascus* and *Ctenomyces* (Eidam) and *Gymnosacus* (Baranetzsky). Most of this work is dealt with in modern text-books with additional cytological details where known. It was assumed that there was a well-marked sexuality in those forms with differentiated male and female organs and a gradual loss of sex, first by the disappearance of the male and, finally, the absence of the female.

O. Brefeld, a former pupil of de Bary, was the chief opponent of the view that the higher fungi show sexuality. He admitted its occurrence in the Oomycetes, but held that it was gradually lost in the Zygomycetes, from which section of the Phycomyces he regarded Ascomycetes and Basidiomycetes to have been derived. He carried on his side of the controversy with a caustic vigour unusual in mycological writings. He accused de Bary of wasting his time and leading his pupils into a blind alley in so obstinately following a chimerical sexuality. He deplored that a school had been able to use up a ravenous activity for twenty years in turning the screw of the ascogonium and that these turns of the spiral had overwhelmed in their whirls the whole of mycology and mycologists.

The controversy continued until the close of the century, by which time cytological methods had been introduced and the venue changed. P. A. Dangeard in 1894 discovered the fusion of two nuclei in the ascogenous hyphae and regarded this as a sexual fusion. It is still a matter of discussion

* Ehrenberg's view was that *Pilobolus crystallinus* is '*ganz auffallend ein halber Syzygites*'.

whether this is the only nuclear fusion or whether, as R. A. Harper first stated in 1896, there is also a fusion of nuclei in the ascogonium.

We have seen how many mycologists have regarded the cystidia in the hymenium of agarics as male organs; Corda, indeed, called them antheridia, then pollinaria, and compared them with separate pollen grains. He stated that a granular liquid oozes out from the open apex and brings about the formation of spores.

A similar idea was contained in a *mémoire* submitted by G. Sicard to the French Academy of Sciences in competition for the Grand Prix des sciences naturelles which was reported on by Brongniart in 1875 on behalf of the commission. The cystidia (antheridia) emit corpuscles enclosing antheridia which fertilize the later-formed basidia—a view which the commission was unable to verify in spite of repeated observations on numerous species with the best instruments in the most varied conditions. The *mémoire* was never published. The same year W. G. Smith gave a similar account of reproduction in *Coprinus radiatus*. He regarded the basidium as female, the cystidium as male. The cystidia are covered with granules. These granules are at first stationary, but in water they begin to revolve and later swim about with great rapidity. 'These spermatozoids attach themselves to the spores, pierce the coat, and discharge their contents into the substance of the spore'. After one or two days 'the spore discharges a cell which becomes free, and this is the first cell of the pileus of a new plant.' Moreover, 'the spores naturally fall to the earth, and with them the cystidia, and it is upon the moist earth that fertilization is generally carried out.' The eddy round the spermatozoids suggested that they were provided with cilia. The worth of the observations may be judged from the statement that a section of the fungus in water collapses and disappears in a couple of hours and bacteria and infusoria appear. 'It seems almost reasonable to believe that the fungus cells themselves become suddenly transformed, and reappear as simple infusoria.' In spite of obvious absurdities, the story seems to have been generally accepted by most mycologists in this country and lingered on for more than twenty years.

H. Hoffmann, 1856, though he agreed with Phoebus that the function of cystidia was protective, used Corda's term pollinaria for them. He was at first inclined to consider that certain nodules or warts he found on the upper side of the ring of *Agaricus* (*Amanita*) *muscarius* which put out vibrating cilia ending in a delicate knob, were sterigmata and spermatia, but eventually decided that in *Agaricus* (*Mycena*) *metatus*, and in other species of *Mycena* and *Collybia*, the conidia on the

mycelium were the real spermatia, though he thought they were not essential for at least the first germination of the spores. He also described clamp-connexions in *Mycena metata* and in *Hymenogaster Klotzschii*, though he did not attempt to suggest their function.

The discovery by W. F. B. Hofmeister (1852) that the sexual act in ferns occurred in the prothallus and not on the sporophyte, turned the search for sexual organs in agarics from the cap to the first stages of mycelial formation*. P. A. Karsten in 1860 described how the fruit-body of *Agaricus* (*Psalliota*) *campestris* arose from an egg-shaped, short-stalked female cell.

In 1886, working with *Agaricus* (*Amanitopsis*) *vaginatus*, he recorded an oblong 'archegonium' on a long stalk separated by a wall. At the same time cylindrical branches appeared only a little thicker than the mycelium. Nothing definite is stated except that these may rest upon the archegonium, but it is implied that there is some kind of fertilization similar to what had been reported in *Erysiphe*. Mycelial outgrowths arose from the stalks and formed the beginning of the fruit-body.

A. S. Oersted, 1865, described similar 'oospheres' formed on small branches of the mycelium of *Agaricus* (*Crepidotus*) *variabilis* and how one or two slender hyphae may, or may not, become applied to them; the oosphere becomes surrounded by hyphal tissue which develops into the sporophore.

With the introduction of Brefeld's culture methods attention was turned to the genus *Coprinus*, and spores were grown in dung decoction. M. Rees, 1875, cultivating spores of *Coprinus stercorarius*, described the rod-shaped conidia (oidia) common in *Coprinus*, which he regarded as spermatia because they were incapable of germination. Finding structures formed of three swollen superposed cells with a spermatium attached to the terminal one he interpreted these as carpogonia. The basal cell afterwards put forth numerous outgrowths which initiated the fruit-body. P. van Tieghem, the same year, obtained similar results with *Coprinus ephemeroides* and *C. radiatus*. He began with single-spore cultures and worked forwards rather than backwards as Rees had done. He found that mycelia were of two kinds, one with carpogonia having a papillate end, the other with conidial rods. 'Le mycelium des *Coprinus ephemeroides* et *radiatus* s'est montré dioïque.' He claimed to have fully proved what Rees thought very probable. This was published on 8 February. On 15 November

* Ehrenberg, 1818, unable to find any trace of a sexual act in fungi except in *Syzygites*, suggested that the sexual function was undertaken by the branched and interwoven filaments of the mycelium (rhizopodium).

the same year* he published a refutation of his results. He decided that the oidia are not spermatia because he had now been able to germinate them and, further, he had obtained fruit-bodies of *Coprinus plicatilis*, *C. radiatus*, and *C. filiformis* in culture where no conidia occurred.

He throws over the carpogonium as a female structure, regarding it apparently merely as a swelling—the oidia are able to fuse both with their own and with other mycelia. Afterwards van Tieghem was the chief supporter of Brefeld in opposing the idea of sex in the higher fungi. In 1875 Rees confirmed the corrections that van Tieghem had made in his first paper, and O. Kirchner obtained similar results regarding the function of spermatia. Eidam, the same year, provided additional proofs in *Agaricus (Psilocybe) coprophilus*, *A. (Pholiota) fascicularis*, and *A. (Pholiota) mutabilis*. J. de Seynes, also in 1875, described an almost spherical vesicle with a long neck as the 'oocyst' of *Lepiota cepaestipes*.

With the end of the year the discoveries ceased, and what had been described was discounted. The mycelium of agarics is generally very narrow, much branched and anastomosed, and, consequently, gives numerous appearances to those indulging in wishful search. The first advance was the discovery by H. Wager in 1892 of the fusion of two nuclei in the basidium of *Stropharia stercorearia*, and the division of the fusion nucleus giving the four daughter nuclei which pass into the spores. M. Bensaude's discovery of heterothallism in *Coprinus* in 1918 gave an unexpected explanation of much that had been puzzling. If van Tieghem, over forty years previously, had disregarded theories and had kept to his single-spore cultures the course of mycology might have run smoother: it was not until 1904 that the phenomenon of heterothallism was first discovered by A. F. Blakeslee working with Mucorineae.

Apart from theoretical reasoning, it was early realized that the spores of the larger fungi give rise on germination† to a mould-like growth, the *Byssus* of many authors. It was frequently sought to homologize the germ-tube with a radicle, but this was part of the old controversy, and, at the time, led nowhere. Strange as it may seem, much more arose from the coining by L. Trattinnick, in his 'Fungi Austriaci', 1804, of the term mycelium for the branching and anastomosing fungal threads, and from his realization of its being as much a part of the fungus as is the fruit-body. He described the mycelium

* On this very day Brefeld published an account of *Coprinus* opposing the view that oidia are spermatia.

† Strictly speaking spores, as they do not contain a germ (embryo), cannot germinate. It is customary and convenient, however, to speak of their first stages of growth as germination.

in a number of species, and recognized that it was the vegetative part of the fungus and not merely the equivalent of a root ; it is as much a fungus as is a phanerogam without flower or seed. It may be perennial or annual, subterranean or superficial. This useful term, appearing at just the right time, greatly influenced the study of mycology. The ambiguous *Byssus* fell into disuse with its implications that all mycelia were morphologically indistinguishable and that agarics were in some way related to the other members of this most diverse genus. C. A. Agardh had introduced the term thallus for the vegetative part of lichens, and this was used by Link and to some extent by Agardh's pupil E. M. Fries.

The time was not ripe, however, for a remarkable paper by I. B. Prevost, published in 1807, entitled 'Mémoire sur la cause immédiate de la carie ou charbon des blés, et de plusieurs autres maladies des plantes, et sur les préservatifs de la carie': it was ignored for half a century. The most careful observers assumed that fungus spores always give rise to a mycelium, but Prevost showed that this is far from true. His descriptions are accurate, and he gives the details of the conditions of his experiments. In a strikingly clear and convincing manner he describes how, in certain 'white rusts' (= *Cystopus Portulacae*, *C. candidus*, *C. cubensis*, and *C. Bliti*), the spores (conidia) formed in chains produce several motile spores (zoospores) on germination. He gives full accounts for the first two species, describing how, after a short time in water, the wide end of the conidium breaks off so that the whole resembles a bottle which has lost a good part of its neck. Inside, a globule appears, then up to six, which unite into a mass and twist and turn about, then separate and take on a quicker movement. 'Ils se meuvent... Ils ne laissent pas plus de doute sur leur nature animale que la plupart des animalcules que l'on a nommés *infusoires*.' The movement gradually slackens, and those zoospores which fix themselves to the surface of the water push out a slender undulating stem. Tulasne was unable to confirm these results at first, but, convinced of Prevost's general accuracy, accepted them 'however marvellous they might be'. They were shown to be correct by de Bary in 1860, and Tulasne succeeded in germinating the conidia of *Cystopus candidus* the following year*.

It was perhaps fortunate that Prevost's investigations received little attention when first published, for at that period it required nothing more than such a clear demonstration of the production of 'animalcules' from spores to revive the

* Prevost first noticed the oospores and oospheres of *Peronospora* spp. by holding infected leaves up to the light.

moribund doctrines which Linnaeus's influence had done so much to further. As it was, the rediscovery of zoospores in *Cystopus* showed that its true position was not in the Uredineae, but with *Peronospora*, in which genus de Bary in 1860 discovered that some species also form zoospores. Moreover, it had its effect in clearing up the problem of *Saprolegnia* and its allies, which were at that time usually thought to be algae. These aquatic fungi had been known for a century. Gruithuisen in 1821 found a species, which he called *Conserva ferox*, on the remains of a snail and figured zoospores escaping, though he does not show cilia, and a second and third zoosporangia within the first. Two years later F. W. Carus described *Hydroneuma* on salamander larvae with spores collecting in the form of a sphere at the mouth of the zoosporangium. Meyen in 1831 and others described the formation and escape of zoospores, and this strengthened many in the belief that the organisms were algae where zoospores had been discovered in several genera since 1807, when Trentepohl observed them in *Vaucheria*. This opinion received further support when A. Braun in 1851 found that the oospores observed by M. J. Schleiden, 1842, and C. Naegeli, 1847, were produced by a well-marked sexual process similar to that known in certain algae. Our present knowledge of the group is based on the excellent work of N. Pringsheim, 1851, and de Bary, 1852. It was the discovery of zoospores in *Cystopus* and *Peronospora*, together with distinct sexual organs, which convinced de Bary of the relation between his Peronosporaeae and Saprolegnieae and led him to erect the major group Phycomycetes in L. Fuckel's 'Symbolae Mycologicae', 1869. But Prevost not only germinated the spores of *Cystopus*. He was the first to describe and illustrate the germination of the spores of certain Smuts and Rusts—all naturally being regarded as species of *Uredo*. He gives a short account of spore germination in *Ustilago Carbo*, mentioning the formation of conidia, but in *Tilletia Caries* he made numerous and accurate observations on the production of the fascicle of terminal primary conidia with their secondary conidia; when Tulasne at last succeeded in germinating the spores in 1855 he was able to add little to the strange story except the formation of H-pieces between the secondary spores—an observation in which incidentally he had been forestalled by Berkeley in 1847. Prevost was puzzled and thought that the secondary conidia were a sort of fruit or a form of *Puccinia*, after flirting with the idea that they might be male organs, or parasites*.

* It has not been thought necessary to mention the various terms adopted by Prevost. His illustrations show what he intended to convey—and 'tufts', 'stems', 'leaves', and so on make his descriptions difficult to follow.

We also owe to Prevost the first account of the germinating teleutospore of *Puccinia graminis*, with its promycelium, sterigmata, and sporidia; and of the uredospore. It may be added that Prevost's description of the infection of wheat by Smut and Bunt and the methods he proposed for protecting plants from disease are far in advance of his period. He was the first, for example, to suggest the use of copper.

The complicated life-cycle of Rust fungi took many years to unravel. The three obvious spore-stages, the uredosorus, teleutosorus, and aecidium were described as separate genera, *Uredo* (1794), *Puccinia* (1794), and *Aecidium* (1791) by Persoon*.

The Rust of wheat must always have forced itself on the attention of mankind from the dawn of agriculture: there are several references to it in the Scriptures and in the classics. It is heteroecious, having its alternate stage on barberry †.

Sir Joseph Banks in 1805 wrote an interesting letter—'A short account of the cause of the disease in corn called by farmers the Blight, the Mildew and the Rust'—which he distributed to those interested in agriculture: it was afterwards republished in several scientific journals. He implies the connexion between the uredospore and teleutospore stages. 'It seems probable that the leaf is first infected in the spring, or early in the summer, before the corn shoots up into a straw, and that the fungus is then of an orange colour; after the straw is become yellow, the fungus assumes a deep chocolate brown.' He thought the teleutospore contained at least a hundred seeds, a sort of 'animated dust', a view practically that of Hooke (cf. Pl. 7, b, which is from a drawing ‡ by Francis Bauer, who was one of Banks's artists). He further says that 'the leaves of the barberry are very subject to the attack of a yellow parasitic fungus, larger, but otherwise much resembling, the rust in corn. Is it not more than possible, that the parasitic fungus of the barberry and that of wheat are one and the same species, and that the seed transferred from the barberry to the corn is one cause of the disease?' In the second edition of this brochure, 1806, there is a letter from T. A. Knight describing some experiments made to test the opinion prevailing very generally 'that barberry trees are injurious to corn', and though his experiments were inconclusive he thought it 'deserves very considerable attention'.

* F. Fontana, in 1767, had described and figured what he thought to be two sorts of Mildew parasitic on wheat—the one black and nail-shaped (teleutospore), the other red and egg-like (uredospore).

† There are several distinct species of *Puccinia* on cereals and a multitude of biological races. The account here refers to the early history of *Puccinia graminis* sens. lat.

‡ Bauer illustrated Banks's letter.

So early as 1660 a decree was promulgated in Rouen directing that barberry plants should be eradicated because of the influence they had on the rusting of wheat, a forerunner of the better-known Massachusetts Barberry Law of 1755. Many attempts were made to get direct evidence of the relation, but it was not until 1864 that de Bary proved it by cultural experiment and microscopical examination. About the same time A. S. Oersted independently proved heteroecism in *Gymnosporangium Sabiniae*, the teleutospores of which occur on juniper and the aecidia (*Roestelia cancellata*) on pear.

There was much controversy in the first half of the nineteenth century about the relation, if any, between the uredospore and the teleutospore. J. B. von Albertini and L. D. von Schweinitz, 1805, because the uredospore always appears before the teleutospore and sometimes a sorus consists entirely of teleutospores, thought that these must develop on the detritus of the former. Corda, 1840, Léveillé, 1846, and Fries, 1849, went further, and held that the teleutospore is parasitic on the uredospore. De Candolle, 1807, agreed with Banks that the two were related, and in 1815 suggested that they might be definite states of the same fungus, as Tulasne fully proved for many species in 1854.

The less obvious spore-stage, the spermogonium, was discovered by Unger, 1833, who named it *Aecidiolum*. M. Meyen, 1844, suggested that it was the male organ of the *Aecidium* which it accompanied. The idea was ridiculed, but in 1851 Tulasne was able to include the Uredineae in those groups of fungi possessing spermatia without implying any significance to these beyond the fact that such spores do not germinate. It was not until 1927 that J. H. Craigie proved that spermatia play a part in the production of aecidia, being the means of bringing together the two sexual phases—sperm cells from spermogonia of one sexual phase fertilizing the aecidium of the other sexual phase.

Tulasne's investigations of spermogonia began in 1851 with the spore-bearing structures on the thalli of many lichens. These had been regarded as parasites, anomalous fruits, and even as other lichens, but he showed that they were the conidial fruits of the lichen. Recognizing their similarity to fungi such as *Septoria* and *Phyllosticta*, he pointed out that these 'Pyrenomycetes' were not autonomous; each *Septoria*, for example, corresponds to a *Sphaeria* which succeeds it and arises from the same mycelium. An investigation of *Tympanis* and *Cenangium* proved that the relation was not one of parasitism. A species such as *Sphaeria Laburni* may have three stages, the ascospore stage, a *Sporocadus* stage, and a *Cystispora* stage. But the different stages are not necessarily associated. He concluded that Sphaeropsidei and Cytisporacei include a multitude of species the perfect stage of

which must be sought amongst the Sphaeriaceae, 'et qui, conséquemment, devront un jour leur être réunis, lorsque des études persévérantes auront bien fait connaître les éléments constitutifs de chaque espèce'.

Tulasne's establishment of the existence of pleomorphism had strange results. He had worked with comparatively large fungi and so was able to convince himself of genetic connexions. But it was different with microscopic forms like yeasts. Kuetzing, as we have seen, believed (1837) that yeast (*Cryptococcus*) developed into *Sporotrichum* and *Mucor*. Turpin in 1837 held that milk globules developed vegetatively into *Penicillium*, but in 1840 he went further in stating that the starch grains from the perisperm of barley were true bulbils which, in favourable conditions, can produce the mother plant, but, if placed in sugar solution, bud and act as yeasts: he named them *Torula cerevisiae*. If conditions permit they develop into *Mycoderma cerevisiae* and later into *Penicillium glaucum*.

Little would have been heard of these statements if it had not been that when later workers competed in the effort to outdistance each other in the search for the solution of enigmatical forms there was a lauding of those who had first discovered the hidden truths.

The first of the new observers was A. Spring, who in 1852 published the results of inoculating a fungus mycelium from a hen's egg into other eggs. He obtained from this *Periconia ramosa*, *P. pulverulenta*, *Aspergillus incrassatus*, *A. glaucoides*, *A. heterocephalus*, *Sporotrichum sulphureum*, *Hemiscyphæ trigemina*, *Mucor oogenus*, *Penicillium glaucum*, and an undetermined mycelium. His illustrations are too poor for an attempt at identification, even if it were worth while.

C. A. E. T. Bail's inaugural thesis, 'De Facece Cerevisiae', 1857, started the avalanche which threatened to demolish the very foundations of scientific mycology. In cooked malt left exposed to the air he found a species of *Mucor*, then *Penicillium glaucum*, and later a second *Mucor*. Placed in beer-wort the first *Mucor* budded, the second *Mucor* became *Hormiscium*. His general conclusion was that most fungi increase by budding if grown in fermentable liquids: it was not possible to decide to what species beer-yeast (*Hormiscium cerevisiae*) belonged, because here reproduction by budding had become hereditary and it is difficult to obtain normal development. It has been fully confirmed that certain species of *Mucor*, e.g. *M. racemosus*, will bud in sugar solutions and, moreover, produce a small percentage of alcohol; this was a real contribution to the subject made by Bail. Three years later he showed himself able to make assertions with no foundations whatever in fact. He identified *Empusa muscae* with *Mucor Mucedo*. If a fly

attacked by *Empusa* is placed in water the *Empusa* develops into *Achyla prolifera*; yeast can transform itself into *Empusa*, and *Isaria farinosa* and *Botrytis Bassiana* belong to the same cycle. The following year he adds that *Mucor Mucedo* in beer-wort grows as *Hormiscium cerevisiae*, and that the *Botrytis* ferments wine. These results were confirmed in part by H. Zabel and wholly by Hoffmann, who added *Ascophora* [*Mucor*] *elegans*, *A. Mucedo*, *Periconia hyalina*, and *Penicillium glaucum* to the series; further, he succeeded in obtaining fermentation of sugar with a number of fungi including Rusts and Smuts, but, strange to say, not agarics. But even these fables seem to make sense when compared with the vast amount of pseudo-scientific drivel perpetrated by E. Hallier. From 1865 until the bubble was finally pricked by de Bary in 1869, a flow of books, pamphlets, and newspaper articles described strange and monstrous stories of the conversion of bacteria into fungi and stressed the necessity of knowing their various appearances because of their importance in some of the most dangerous human diseases; Hallier's name became world famous. He had his proper apparatus which kept away alien organisms from his cultures, but he never realized that the cultures themselves were contaminated before being enclosed. He had, for example, seven series of *Penicillium* and of *Aspergillus glaucus*. It would be useless even to summarize his results. He went from strength to strength until finally Hoffmann, one of his strongest supporters, but whom he had chided for misrepresenting his views, said that if he continued his cultures on starch with the zeal and judiciousness that had guided him up to then, without doubt he would reach the certainty that all fungi are only forms of his *Micrococcus* and *Penicillium*, and that would not only simplify and facilitate the study of mycology, but would enhance his reputation among those unable to judge matters for themselves.

Hallier's views on cholera were that this disease was produced by *Urocystis*, which is part of the cycle *Mucor-Penicillium-Tilletia*. This *Urocystis* occurs on rice in India, but does not occur in Europe because of its temperature requirements; it develops well in the human intestine, however, which has almost exactly the temperature of India. The more investigations he recorded the wilder the statements*.

* M. J. Berkeley, in his Presidential Address to Section D (Biology) at the British Association Meeting at Norwich, 1868, comments on 'the theory of Hallier respecting the origin of certain diseases. His observations were at first confined to Asiatic cholera, but he has since made communication to the authorities of the Medical Department of the Privy Council Office, to the effect that in six other diseases—typhus, typhoid and measles (in the blood), variola, variola ovina, and vaccinia (in the exanthemes)—he has found certain minute particles which he calls micrococci, which under culture-experiments give, for

Fortunately, de Bary was at that time writing his 'Morphologie und Physiologie der Pilzen, Flechten und Myxomyceten', 1866, and therein he pointed out the gross errors committed by the Hallier school. The need for beginning from a single spore or from spores all of one kind and the necessity of proving genetic connexion had been omitted: the protection of a mixed infection from outside contamination was an unnecessary precaution. Indeed, de Bary's criticisms were based on the principles followed to-day in all methods of pure culture, and which he himself had adopted in proving that *Aspergillus glaucus* and *Eurotium herbariorum* are different stages of the same fungus—a result which, together with similar ones (1853-4), had done much to stimulate the pleomorphists who completely misunderstood the attitude Tulasne and he adopted. Bail, Hoffmann, and O. W. Thomé at a meeting of German Naturalists at Frankfurt in 1867 reiterated their views with appropriate additions, and M. Woronin upheld de Bary's criticisms. Hallier published his 'Phytopathologie' in 1868 and de Bary returned to the attack. After this date the crazy superstructure began to topple. True Hoffmann in the following year listed nine fungi as well as bacteria which gave rise to the yeast of beer, and J. B. Carnoy followed in 1870 with the statement that he could state categorically that all fungi

each of the above-mentioned diseases, a constant and characteristic fungus. He states that in variola he gets the hitherto unknown pyrenidia of *Eurotium herbariorum*; in vaccinia, *Aspergillus glaucus*, Lk.; in measles, the true *Mucor mucedo*, of Fresenius; in typhus *Rhizopus nigricans*, Ehrenberg; and in typhoid *Penicillium crustaceum*, Fries. He adds that the culture-experiments, especially with the variola diseases, have been so very numerous as to exclude from the results all supposition of accident—that different districts, different epidemics and different times have given identical results. I am anxious to say a few words about the subject, because most of the reports which have been published in our medical journals give too much weight, in my opinion, to his observations, as though the matter had been brought to a logical conclusion, which is far from being the case. I am happy to say that it has been taken up by De Bary, who is so well calculated to give something like a conclusive answer to the question, and also that it has been taken in hand by the medical authorities of our army, who are about to send out two of their most promising young officers, perfectly unprejudiced, who will be in close communication both with De Bary and Hallier, so as to make themselves perfect masters of their views, and to investigate afterwards the subject for themselves.' After a criticism of Hallier's method of investigation he ends, 'I might enter further into the matter were it advisable to do so at the present moment. All I wish, however, is to give a caution against admitting his facts too implicitly, especially as somewhat similar views respecting disease have lately reached us from America, and have become familiar from gaining admittance into a journal of such wide circulation as "All the Year Round", where Hallier's views are noticed as if his deductions were perfectly logical.'

cultivated in certain conditions become transformed into a *Penicillium*, which is almost identical everywhere and therefore is widespread. But these were the final rumblings of phantasy, and pleomorphism took its proper place in scientific mycology. Hallier even so late as 1895 in his 'Die Pestkrankheiten (Infectionskrankheiten) der Kulturgewächse' returned to the attack, though with much modified claims, fortifying himself by stating that he had followed strict bacteriological methods in full accord with those of R. Koch. But it met with a worse fate than his previous writings; it was ignored.

It was long a problem whether spores on germination give rise to the same species of fungi as that from which they are derived. The older experiments were not conclusive and depended more on analogy with the seeds of flowering plants than on proper demonstration.

The first attempt to follow a life-history from spore to spore by a method which is not open to criticism, appears to be that of J. Schilling, who, in 1827 traced the development of *Aspergillus glaucus* in culture chambers under the microscope. This first experiment on pure culture was not followed up for many years, presumably because its significance was not realized; owing to the frequency of fusion between mycelia it was often assumed that several spores were necessary for the production of a mature fruit-body.

No real advance was made until Brefeld in 1868 pointed out the necessity of sterilizing culture media and of following the development of single spores. Criticizing the pleomorphists he said that inoculation without previous sterilization is on a par with a man already soaked putting on a rain-coat for protection against the last drops of rain; if one does not work with pure cultures one gets only nonsense—and *Penicillium glaucum*. In a long series of researches ('Botanische Untersuchungen', I-XV 1872-1912) he applied his principles in tracing out the life-histories of a large number of fungi. Brefeld used gelatine to solidify liquid media; 'nutrient gelatine' as a solid medium was introduced by Koch in 1881, the wife of his associate W. Hesse suggesting the replacement of gelatine by agar-agar the following year. Koch's assistant R. J. Petri in 1887 devised the Petri dish to replace the flat plates formerly used.

J. Lister's dilution method for obtaining single bacteria, 1878, and Koch's poured plate method, 1883, were of equal value in mycology, for so far as regards cultivation *in vitro* the principles are the same; the difference in practice is that for the most part different media are used because of the different nutritional requirements of the organisms. With

the introduction of what are usually called bacteriological methods, the study of those species which can be grown in pure culture proceeded apace, and many problems which had puzzled mycologists for a century or more were solved. Some groups of fungi, however, e.g. Rusts and Mildews, have not been grown in this way and others, e.g. Basidiomycetes, usually form abnormal fruit-bodies or none at all. Here other criteria have to be used, but the fundamental facts learned from pure culture methods enable them to be applied with a considerable degree of certainty.

Fungi as parasites are of great importance economically and so have forced their activities on the attention of man. Many of the older ideas have been mentioned in passing, but a few general remarks may be given without attempting a historical treatment. Blasting and Mildew were signs of Jehovah's wrath, and Mildew was averted by Robigus, the Roman God who was propitiated on Robigalia, the 25th of April. The effect of frost, rain, dew, east wind, superfluous sap, insect bites, lack of fertilization, and other such influences on plants were repeatedly put forward as the cause of disease. There was difficulty in distinguishing between the diseased plant and the fungus causing the disease. Thus J. A. Planer 1709—'De Ustilagine frumenti' (Pres. R. J. Camerarius),—speaking of Smut in corn writes, 'Id, quod passum fuit triticeum, discitur conversio in pulverem atrum: Hinc est *ustilago*, Botanicis frugum non species, sed vitium, morbus & pestis.'

Similarly, ergot (*Claviceps purpurea*) in A. Lonicer's 'Kreuterbuch', 1582, is in an appendix on rye, and was for a long time regarded as diseased rye grain, J. Thalius, 1588, suggesting that the grain was forced to grow out because of the excessive production of sap after much rain followed by hot weather. This view was adopted by C. Bauhin, who gave it the name *Secale luxurians*. L. C. Hellwig, 1699, recognized the conidial stage (honey-dew, *Sphacelia*) as the cause of ergot. C. J. Geoffroy, 1771, thought ergot resembled a fungus rather than a rye grain, and Münchhausen, 1764, had no hesitation in regarding it as a fungus, and most later writers accepted this interpretation.

What appears to be the first general treatment of plant disease was the essay 'Observations sur les maladies des plantes' by Tournefort in 1705. He classified diseases into five groups caused by (1) too great abundance of sap; (2) absence of or too little sap; (3) bad qualities acquired by the sap; (4) unequal distribution of the sap in different parts

of the plant; and (5) external accidents; but fungi are mentioned only incidentally and no significance is attributed to them. Similarly, in a thesis by C. S. Eysfarth (resp. P. C. Müller) entitled 'De morbis Plantarum', 1723, the physiological aspect of disease is foremost and is considered at the period of germination, during vegetative growth and at maturity. Again internal and external causes are mentioned, but the views of Marsigli and Lancisi about fungi are adopted and consequently they receive merely passing notice.

At the time of Linnaeus there was an attempt to name and classify diseases much in the same way as plants themselves were classified. We have seen how Linnaeus himself came to grief in following Münchhausen in the belief that *Ustilago* consisted in reality of 'animalcula viva'. As Linnaeus was a medical man it was not surprising that his chief attention was paid to human disease, and in his 'Exanthemata Viva' in 1757 he propounded the view that the causes of diseases of the type scabies, dysentery, whooping cough were to be ascribed to the presence of certain parasitic animalcules, partly visible to the unaided eye, and whose presence was thus fully established, and partly as yet unperceived, although for good reasons, undoubtedly existing, and in 'Mundus invisibilis' he went so far as to consider it was certain that all putrefaction depended upon the activities of 'nothing but living particles'.

J. C. Fabricius, a pupil of Linnaeus and an outstanding entomologist, in an essay on phytopathology, 1774, protested against the ideas put forward by Münchhausen and also against Gleditsch's theory that disease was caused by sowing unripe grains; clean grains give clean crops whether mature or not. Neither does night frost nor fog cause Mildew in hops, for if it did all plants would be affected. Independent species of fungi are the cause of such diseases.

It was a long time, however, before such ideas were accepted. Plant diseases were classified in the manner customary for human diseases doubtless because so many investigators had had medical training.

The beginning of the nineteenth century was marked by an interest in the physiology of plants, and there was again a tendency to regard parasitic fungi as originating from the diseased host tissues. Thus F. J. A. N. Unger in his famous 'Die Xantheme der Pflanzen', 1833, calls parasitic fungi entophytes or disease organisms. Disease is due to the absence of certain substances from the sap brought about through internal disintegration of the processes of nutrition, and parasitic fungi arise from this morbid sap on the still living host tissues. Unger's views dominated the thought of his period,

and the fact that they fitted in with Fries's statements about parasitic fungi *, doubtless influenced opinion.

The great damage—even famine—caused by the potato disease in the early forties of last century led to much investigation, for many scientific bodies and several governments offered rewards for the unravelling of the cause of the destruction, and for means of preventing it. Controversies raged about the nature of the relation between fungus and host-plant, but gradually the view that 'the decay is the consequence of the presence of the mould, and not the mould of the decay' (Berkeley, 1846) came to the fore. The researches of Tulasne, de Bary, and others on the structure and development of fungi during the next decade cleared up the problem, and in his 'Outlines of British Fungology', 1860, Berkeley could write: 'Fungi were long regarded as the mere creatures of putrescence, and therefore as the consequence, not the cause of disease. A more intimate acquaintance with their structure and habits has, however, removed much of this prejudice, and almost everyone is now ready to acknowledge what a weighty influence they have in inducing diseased condition, both in the animal and vegetable world.'

From this time the part played by fungi in causing plant disease was clear. The study of the various factors influencing infection, immunity, and remedial measures gradually passed from the sphere of botany and even of mycology, and became a specialized discipline, which, for economic reasons, now attracts the majority of those receiving a botanical training.

The common knowledge of bacterial diseases of man nowadays makes it seem strange that it was not until the work of Pasteur †, Lister, and Koch that the importance of bacteria in this connexion was understood. Indeed, in the first half

* 'Hypodermii (Entophyti). Char. Vegetatio propria nulla. Sporidia ex anamorphosi telae cellulosa plantarum vivarum orta; sub earum epidermide enata et per hanc erumpentia.

Obs. Ex altera parte sunt exanthemata plantarum: ex altera simul vegetationem propriam offerunt. Sunt itaque fungi inferioris ordinis, a matrice pendentes, absque omni propagatione per sporidia; sed e fungorum censu prorsus eos excludere non licet... Ubi nulla propagatio per sporidia, ibi etiam nullae species sensu vulgari! Singulus typus est genus, pro singula planta novam enitens speciem.'—Fries, *Systema*, III (1832).

† Pasteur was a chemist by training, and though he made contributions to biology of such importance that his name is a household word, he seems to have been content with casual identifications. Pasteur 'der bald von *végétaux cryptogames microscopiques*, bald von *animalcules*, von *Champignons* oder von *Infusoires* spricht, "*Torulacées, Bacteries Vibrioniens, Monades*" ohne scharfe Unterscheidungsmerkmale auführt, die nämlichen oder doch verwandte Gebilde auch als *Mycoderma*, als *Mucor's Mucidinées* oder also Hefe (*levure*) bezeichnet.'—Cohn.

of last century fungi were regarded as far more important as human and animal pathogens.

This was due partly to the recognition and description of several genera of the ring-worm type—*Achorion* Remak (1840, but first discovered by J. L. Schoenlein in 1839), *Microsporon* Gruby (1844), *Trichophyton* Malmsten (1845, described by L. J. Gruby in 1844), and 'thrush' first recognized as a fungus independently by Berg in 1844 and Gref in 1842 and named *Oidium albicans* Robin. The position in 1853 is shown clearly in C. Robin, 'Histoire naturelle des Végétaux parasites', which deals with those forms which grow on man and living animals; it contains no mention of bacteria.

At that period microscopic organisms had to be seen in mass before their significance was considered; otherwise it was the old *Corruptio unius, generatio alterius*—or degeneration, miasm, communicable chemical derangement or an act of God.

There were many suggestions of the germ theory of disease—some, indeed, remarkable in their scope and accuracy,—but they lacked the proof of observation and experiment. Fermentation, spontaneous generation, putrescence, and the specificity of parasitic organisms all had their place in the theoretical discussions.

The first satisfactory demonstration of the capability of an organism to enter another organism and cause disease was made by A. Bassi, who, after working for many years, published his results on the silk-worm disease known as 'musccardine', 'calcino', etc., in 1835. The dead insect becomes covered with the chalk-like growth of *Botrytis Bassiana*. Bassi showed conclusively that the disease is contagious and that it can be transmitted to healthy insects, the fungus becoming apparent only after they have succumbed.

We thus again come back to the question of entomogenous fungi. Their study has added much to systematic mycology in the century that has elapsed since Bassi's discoveries. Montagne and Robin in 1849 described the 'production parasite' on three species of *Branchius* figured by Rouget three years previously, as *Laboulbenia Rougetii*. This remarkable fungus was the first of the Laboulbeniales, one of the most interesting groups of fungi known to us chiefly by the classical researches of R. Thaxter, whose magnificently illustrated 'Contributions to a Monograph of the Laboulbeniaceae' (I-V, 1896-1931) so added to the number of genera and species that the group may be regarded as one of the most thoroughly investigated though amongst the least known to mycologists.

In this historical sketch many aspects of the mycology have been omitted, and others treated either at greater or shorter length than their importance might seem to warrant. To

some extent this has depended upon whether or not there was a readily available account; the omissions are deliberate, for many matters fall outside the scope of what I had in mind. Mycology is a study with many facets, reflexions on which would make a full man.

APPENDIX.

Correspondence between Linnaeus and Münchhausen.

The correspondence begins with a letter from Münchhausen dated Steyerberg 18 April 1751.

J'ai fait jusqu'à 200 desseins de FUNGIS que j'ai amassés tous moi-même l'année passée.

Ibidem 9 Dec. 1751.

Jam ex quatuor mensibus Ustilago frumenti me occupat, et plus quam 200 Experimenta demonstrant pulverem illum fuscum esse ovula Insecti cujusdam corpore nudo artubus destituto, ovato oblongo. ovula hæ in humiditate explicantur; animal succum plantae haurit, pro formandis seminibus destinatum, et in fine ovula relinquit.

Clavi !/?/ vero quos Dn. Needham examinavit ab Ustilagine diversi, et substantiae sunt Spongosae vel fungosae, ac ejusdem generis cum fungis nigris qui in truncis plantarum e.g. in Brassica nascuntur, et ex humiditate oriuntur; Anquillae Needhamii in illis mihi videntur accidentales et ex humiditate oriuntur; Anquillae Needhamii in illis mihi videntur accidentales et ex corruptione ortae.

Schwobberae 19 Jun. 1752.

Nonne fortasse Lichenes inter plantas terrestres idem erunt, quod Lytophyta in plantis maritimis?

Ibidem 7 Oct. 1752.

De reliquo Experimenta magis magisque me convincunt, Fungos et Lichenes in terra et arboribus idem esse quod Lytophyta in mari: Gleditschii flores et semina fungorum non magis probant, quam Marsilii flores Lytophytorum.

Ustilaginem effectum esse insectorum, omnia experimenta confirmant; curiosissimus causam inquiri, cur numquam in Secali inveniatur, cum in aliis omnibus frumentis adsit; etiam in junco quodam ustilaginem inveni. Pulverem Lycoperdorum idem esse aestimo.

Clavi autem quos in secali hordeo Lolio et Specie quadam graminis vidi, nihil aliud sunt quam genus fungorum; qui ex putredine oriuntur si pluviae semina putrefaciunt, quomodo oriantur et indies crescant. hoc anno pluviis abundante, clarissime vidi.

Steyerbergae 7 Mai, 1753.

Si Lithophyta vera sunt producta animalium in mari: Fungos et Lichenes idem esse in terra et arboribus puto; de Fungis imo id certissimum esse credo, ex pulvere Lycoperdi nova animalia generari, et illum uti pulvis ustilagensis vera ovula esse, saepissime vidi et omnia experimenta id probant.

Schwöbberae 26 Sept. 1754.

Fungi, Lichenes, corallia in Systemate meo dabunt Regnum quasi intermedium inter Regnum animale et vegetabile, an *sertularia* omnia vel nonnulla illis adnumerem? dubius adhuc sum. Fortasse *Opus Ellisi* Londini proxime edendum novas subministrabit observationes; qui omnes illas plantas opus animalium esse adserit, sed ex mea quidem sententia distinguendum est, an planta semel a semine enata evadat

domicilium insectorum aquaticorum, an vero sic putata planta sit opus omnino ab insectis exstructum? uti cochleae a limacibus vi animae animalis exstruuntur.

Sic dicta semina Fungorum et Lycoperdi ovula vera insectorum esse omnino persuasus sum. De Lichenibus dubius quodammodo haereo: sed cum nulla omnino vestigia florum in illis inveniam, ex analogia cum corallis, illa esse corallia Terrae credo.

Linnaeus to Münchhausen Upsaliae 21 Dec. 1764 (possibly never sent).

Milleis cogitavi de magno Tuo invento s. de *ustilagine* Tritici Hordeique, de qua mihi quondam perscripsisti, nec potui haec capere; in misso hoc Tuo opere legi historiam et stupefactus fui; exspecto avidissime aestatem ut propriis oculis videam num vivant: num se moveant; utrum sint vermes vel insecta, et ad quem ordinem aut genus amandanda.

Linnaeus to Münchhausen 7 Octobr 1766.

Milleis cogitavi de stupendo Tuo invento, de farina scilicet *ustilaginis* viva; nunc auxisti id *Lycoperdi* farina et per consequens reliquorum Fungorum. De hoc argumento jam cogito die nocteque. Fateor quod Fungi nimis recedant ab omnibus aliis plantis. Video Coccum gravidum [?] figi in ramulo et uti Lycoperdon, totum resolvi in ova et pullos. Majus est hoc inventum quam forte multi capiant; ita comparatum est cum Naturae palatio, ut si quis modo valeat aliquam in ejus aede januam ante clausam reserare, videbunt omnes per eam intrantes Templum vastissimum, ornatum undique summis Ejus miraculis, qui hoc condidit; quis credidisset Polypos aperire viam ad omnia Lithophyta, Zoophyta &c. quis speraverat tam multa de Succini electricitate. aperuisti januam, nullus etiamnum ausus est intrare templum, attoniti stamus adhuc in janua.

Posui Farinam nigram *ustilaginis* in a./qua/ naturaliter tepida, ubi exclusa in viva animalcula me summa laetitia afficit. Nec possunt mei oculi hoc jucundo spectaculo sufficienter satiari. Brevi dabo de hoc Tuo stupendo invento dissertationem et invitabo quotquot potero, ut in hoc argumentum ulterius insistant; nec dubium quin caussa morborum contagiosorum per hoc illucescat.

The same to the same. Upsaliae 15 April 1767.

Quo magis cogito de stupendo TUO invento, de Fungorum seminibus animatis, eo majus mihi hoc occurrit hoc inventum, ut nihil magis optarem quam quod vel IPSE vel alius huic negotio par, in se sumeret hoc inventum ulterius prosequendi, et imprimis in morbis contagiosis, quo nova lux accenderetur in tota Medicina, quae extenderet suos radios ad omnes gentes generis humani. Hoc argumentum tetigi in dissertatiuncula, me absente misere impressa, ut pudeat mittere. Si TIBI Generosiss. D: Baro occurrat *Mucor* iste *septicus*, qui corrodit pavimenta et domos ligneas, quaeos inspicias numne quod corrodat ligna totum constet ejusmodi vermiculis. Optarem magnopere scire num ista animalcula infusoria, quae observantur dum Piper aliaque aromata per aliquot dies contineantur in aqua tepida, sint aliud quam *Mucoris* semina animata; vel etiam ista animalcula, quae in omni aqua impuriore, quae per aliquot dies relicta stetit, occurrunt, sint tantum fungorum semina. Praevideo fore quod si aliquis lynceus se totum consecraret huic argumento, infinite multa illustraret, quae etiamnum latent, cum natura nulli major, quam in minimis.

Münchhausen to Linnaeus Hannoverae 22 Oct. 1769.

Tibi meritas gratias agere pro laude illa, quam mihi in Mund/o/ Tuo invisibili tam gratiose tribuis. Applausus tanti Viri merito est maxima ad ultiores progressus excitatio.

EXPLANATION OF PLATES

PLATE 5.

- a. R. Hooke, 'Micrographia' (1665), Pl. 12, f. 2, illustrating 'blue Mould' [? *Mucor*].
- b. . . . Pl. 12, f. 1, illustrating 'Plant growing in the blighted or yellow specks of Damask-rose-leaves, etc.' [*Phragmidium*].
- c. M. Malpighi, 'Anatome Plantarum' (1679), Pl. 28, showing *Mucedo* [*Rhizopus*, *Mucor*, etc.] and the mycelium of *Fungus*.
- d. L. F. Marsigli, 'Dissertatio de Generatio Fungorum' (1714), Pl. 10, explaining the origin of *situs* from plant remains in a mass of earth and dung. The lower portion of the top figure is copied in N. J. de Necker, 'Traité sur la Mycétologie' (1783), f. 14, to illustrate his *carcithe*.
- e. J. P. de Tournefort, 'Observations sur la naissance et la culture de Champignons'. Mém. l'Acad. Sci. Paris (1707). The two top figures show the construction of mushroom beds; the smaller figures the development of mushrooms from mycelium.
- f & g. P. A. Micheli, 'Nova Plantarum Genera' (1729), Pl. 73. The enlargements show spores 'singillatim dispersa' (G) and 'quaterna sibi contigua' (H) in *Fungus*. The 'flores apétale' are shown single (B) and in groups (C) on the gill edges; they are shown separately on the plate, (D) and (E). [None of these figures appears on the original drawing for the plate, which is at the British Museum.] The figure in the bottom left corner shows growth in horse-droppings and the one above it cystidia on the gill surface. (Fig. 2 is *Pleurotus Eryngii*.)

PLATE 6.

- a. P. A. Micheli, Pl. 91. *Aspergillus* above, *Botrytis* below.
- b. . . . Upper half of Pl. 95. *Mucor*. The figures A, B, C, illustrate Micheli's experiments on the sowing of 'seeds' of *Mucor*, *Aspergillus* and *Botrytis*. (The figure is identified with Hooke's Pl. 12, f. 2. The plate is dedicated 'Auspiciis Rev. Roberti Uvedale LL. Doctoris Angli'.)
- c. . . . Upper half of Pl. 102. *Tuber*. Figs. E, F, G show asci with 2, 3 and 4 spores.
- d. J. Hedwig, 'Descriptio et adumbratio microscopico-analytica Muscorum Frondosorum', II (1789), Pl. 3. *Octospora scutellata* (above), and *O. hirta* (below). This is the first of the plates showing asci and internal spores. [The internal spores do not show clearly in the reproduction.]
- e. A. C. J. Corda, in J. Sturm's 'Deutschlands Flora', III, 14-15 (1837). Pl. 58. *Clavaria pistillaris*. 'Asci' are figured for this Basidiomycete.
- f. . . . Pl. 49. *Agaricus* (*Coprinus*) *micaceus* with spores shown in the corners of a net-work to explain the quaternate arrangement of spores in *Coprinus*. (Fig. 7 shows the 'anthers' [cystidia].)

PLATE 7.

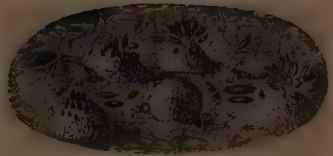
- a. C. G. Ehrenberg. 'Syzygites, eine neue Schimmelpilzgattung etc.' in Verhandl. Ges. Naturf. Freunde, Berlin. I (1820). Stages in formation of zygosporos.
- b. Francis Bauer. One of the original drawings in the British Museum (Nat. Hist.) illustrating 'Diseases in Corn'. The teleutospores at the top right, show 'seeds' escaping.
- c. M. J. Berkeley 'On the Fructification of the Pileate and Clavate Tribes of Hymenomycetous Fungi,' Ann. Nat. Hist. I (1838), Pl. 5. Figures of basidia in *Craterellus*, *Coprinus*, *Gomphidius*, *Pleurotus*, *Cantharellus*, *Boletus*, *Hydnum*, *Thelephora*, *Clavaria*, *Calocera*, *Phlebia*. The three figures at the bottom right are of utricles (cystidia).

- d. J. H. L  veill  . 'Recherches sur l'Hymenium des Champignons', Ann. Sci. Nat. s  r. 2, VIII (1837). Pl. 8. Figures by L  veill   (other three plates are by J. Decaisne). Section of gills of *Agaricus* (*Coprinus*) *micaceus* in centre showing projecting cystidia and basidia which are shown enlarged above. Other basidia are those of *Lactifluus* [*Lactarius*], *Hydnum*, *Daedalea*, *Boletus*, *Cyphella*, *Polyporus*, *Thelephora*, *Schizophyllum*, *Pistillaria*, *Clavaria* and *Dacryomyces*.
- e. J. Torrubia. 'Aparato para la Historia Natural Espa  ola' (1754), Pl. 14. Plants growing from wasps. [? *Cordyceps sphecophila*].
- f. P. Boccone. 'Museo di fisica etc' (1697). P. 300, f. 2. *Tuberaster fungos ferens* [*Polyporus tuberaster*].





a.



b.



c.



d.



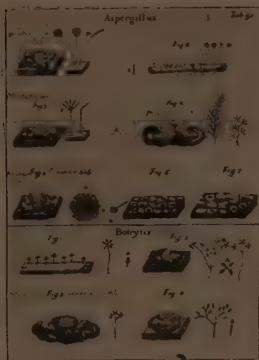
e.



f.



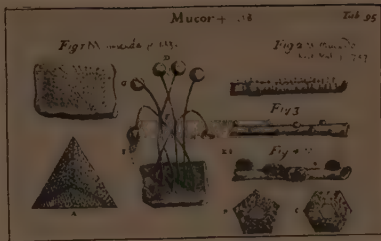
g.



a.



C.



b.



d.



e.



f.



a.



b.



d.



c.



e.



f.

